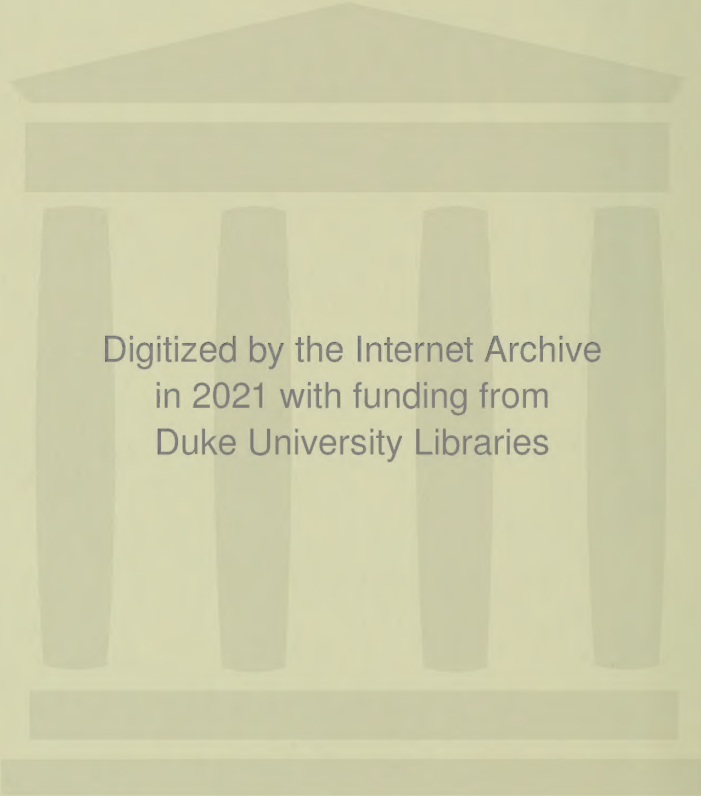
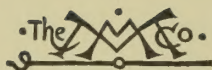




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BUMBLEBEES AND THEIR WAYS



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Queen of *Bombus ternarius* sipping nectar. About
natural size,

BUMBLEBEES and Their Ways

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With a Foreword by

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Illustrated

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TO MY TEACHER AND FRIEND,
WILLIAM MORTON WHEELER

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FOREWORD

Though the bumblebees constitute only a small group of a few hundred species, they are nevertheless among the largest, most conspicuous and abundant insects, at least in north temperate and boreal regions. They are also, owing to their industry in pollinating certain useful plants like the red clover, of no little economic importance. We should therefore expect to find among the annals of entomology a rich store of accurate information in regard to their life-histories and behavior and some general familiarity with their more salient characteristics among the intelligent public. As a matter of fact, however, our knowledge of the bumblebees and their ways is only just beginning to acquire satisfactory consistency. Neither the public nor the great majority of entomologists, in America at least, possesses more than the most superficial acquaintance with these remarkable and beautiful insects, which throughout the summer months enliven every garden, field, and roadside with their splendid velvet liveries and their humming, bustling preoccupation with the flowers. We are all impressed by the drollness of this fervid activity in creatures so clumsily built and clad in habiliments better suited to a more indolent and Sybaritic existence, but this is because we are so used to finding industry and bustle in our fellow men most frequently associated with a lithe and lightly clad physique. In the fields, moreover, we are observing only the foraging instincts of the bumblebee and therefore merely a fragment of its whole behavior pattern. Its more significant be-

havior, the construction of its waxen cells, the rearing of its young and, in fact, its whole peculiar social economy, are concealed from observation in the dark recesses of the nest and guarded by the formidable stings of the workers and queen. It is manifestly the fear of these stings that has retarded the growth of our knowledge of the really significant, intimate behavior of the bumblebees. We should therefore admire the courage no less than the observational skill of the small number of investigators spread over two centuries—Réaumur, Pierre Huber, Hoffer, W. Wagner, Sladen, Lie-Pettersen, Frison, and the author of the present volume—who have given us nearly all the information we possess concerning the life-histories and behavior of the Bombidae.

In this volume Dr. Plath has presented in a very attractive though highly condensed form the results of his study during thirteen consecutive summers of the thirteen species of true bumblebees (*Bombus*) and the four species of parasitic bumblebees (*Psithyrus*) known to inhabit New England and other parts of North America. His early acquaintance with the common bumblebees of Central Europe and his careful reading of the pertinent literature—listed as a most useful bibliography at the end of the volume—have enabled him to select for special investigation several interesting problems which had been either incorrectly formulated or only partially solved by previous workers. Doctor Plath's great success in elucidating the different life-histories and social behavior of the more common North American bumblebees is due, perhaps, quite as much to his development of simple but adequate methods of handling the bumblebees in artificial nests as to his unusual enthusiasm, patience, and skill as an observer. His technique, described in the tenth and eleventh

chapters, will, of course, be of the greatest assistance to anyone who may wish to repeat his observations on the species treated in this volume or to undertake original investigation in other geographical areas. There is here a promising opportunity for the young entomologists of our Far Western States as well as for those of Central and South America, because our ignorance of the life-histories and behavior of almost all the Bombidae peculiar to these regions is nearly complete. It will be interesting to ascertain whether all these species can be fitted into the significant ethological classification outlined in Dr. Plath's thirteenth chapter.

Among the new and more striking results of Dr. Plath's investigations, we may call attention to the pronounced phenological and behavioristic differences which he has detected in the different species, the singular methods employed by *Bombus fervidus* in dealing with its enemies, the simple and very plausible explanation of the "trumpeter" bee's behavior, formerly interpreted in such an anthropomorphic manner, and especially the account of the parasitic activities of the species of *Psithyrus*. This last is a notable contribution not only to general parasitology but also to the theory of social parasitism in particular, owing to the analogies which it suggests to the behavior of several workerless and parasitic genera of ants (*Anergates*, *Wheeleriella*, etc.) and the two known workerless species of *Vespa* (*V. austriaca* and *V. arctica*).

Accurate observations on the bumblebees are of unusual evolutionary interest, because these insects so clearly represent one of the simplest, most primitive, and archaic types of social life among the bees and the social Hymenoptera in general. Since forms closely related to our modern bumblebees occur in the Baltic amber, we may assume a

persistence of these primitive social patterns since early Tertiary (Lower Oligocene) times.

One of the archaic characters of the bumblebee colonies is their small size, or meager population, and one of the great difficulties in the investigation of the honeybees has always been the large size of their colonies. The same is true also of most of the stingless bees (*Meliponinae*) of the American tropics. In the bumblebee colony, however, the individuals are not only larger than any other social insects, but sufficiently limited in numbers to permit closer observation and easier experimentation. Furthermore, the complete social development, or ontogeny of the bumblebee colony, like that of the social wasps and most ants, may be readily observed under proper artificial conditions from its inception in the fertilized queen to its dissolution in the late summer or autumn.

Doctor Plath is to be congratulated on having produced a vademecum which every nature lover will wish to possess. It both fulfills the function of an accurate taxonomic guide to our common North American bumblebees and constitutes, in its emphasis on the behavior pattern of each species, an outstanding example of the many up-to-date contributions with which the younger entomologists are steadily enriching their science.

WILLIAM MORTON WHEELER.

PREFACE

In Franklin's monumental work, "The Bombidae of the New World," we have a taxonomic outline of our American bumblebees, equal, if not superior, to similar works on the European species. One is rather disappointed, however, on comparing our knowledge—or rather lack of knowledge—concerning the habits of our American species with the interesting accounts of the European species by Hoffer and Sladen. What we do know about the habits of the approximately one hundred bumblebee species thus far recorded from the New World we owe chiefly to Putnam, Coville, Hudson, von Ihering, Franklin, Rau, and Frison; but all that has been accomplished up to the present time represents merely pioneer work when one considers what a multitude of secrets still lie hidden in the intricate social life of these fascinating and useful insects.

In the following chapters, I have included some of my earlier observations and experiments which have been published in various biological journals during the past twelve years. In all such cases the articles incorporated have been thoroughly revised, and, for the most part, considerably shortened. The greater portion of this volume, however, consists of material not heretofore published. It is my ambition and hope to continue the investigations of the past thirteen summers by devoting at least three months each year to the study of bumblebees in various parts of the world, and I shall be gratified if my efforts should prove a contributing factor in bring-

ing forth a few co-workers among the younger naturalists.

The work which finally resulted in this book would probably never have been undertaken and brought to completion without the sympathetic and inspiring interest of Professors Joseph Bequaert, Charles T. Brues, and William M. Wheeler of Harvard University. To these three learned scholars I wish to express my profound gratitude. For the drawings and colored plates I am indebted to Dr. Clyde E. Keeler of the Harvard Medical School. I should also like to thank the following for their kind assistance: Professor William G. Aurelio, Professor Mervyn J. Bailey, Miss Lena Berman, Dr. Donald Cameron, Professor Alcide de Andria, Dr. J. H. Franklin, Dr. T. H. Frison, Miss Mildred Hatch, Dr. D. Kostoff, Dr. Z. P. Metcalf, the late Dr. Lyman C. Newell, Dr. A. L. Reagh, Professor O. A. Stevens, Dr. L. H. Taylor, the late Miss Jeanette Thurston, and Dr. William M. Warren.

These acknowledgments would not be complete without mentioning the service of my wife, Aurelia S. Plath, who has aided me greatly in editing the manuscript and in proofreading.

O. E. PLATH.

Boston, Mass., February 3, 1934.

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BUMBLEBEES AND THEIR WAYS

INTRODUCTION

The foundations of this book were laid during my early boyhood in Central Europe, after my interest had been aroused by the discovery that bumblebees make delicious honey. Having repeatedly observed the activities of a neighboring bee-keeper, I thought it might be possible to transfer bumblebee colonies to artificial domiciles, and thus have honey available at all times. This idea was carried out a few weeks later, and during that and the two following summers about twenty-five bumblebee colonies belonging to six European species, were placed in cigar-boxes and transferred to the family garden. The method employed in "transplanting" these colonies was rather crude, and so it happened that I was sometimes severely punished by the more vindictive species.

Although these early attempts to "keep" bumblebees were made primarily for the purpose of obtaining honey, they also yielded some valuable scientific by-products, for in this way I became intimately acquainted with many of the activities of these insects, one of my favorite pastimes being to watch the queen oviposit. My interest in bumblebees constantly grew, and when I found that even my teacher in natural history knew very little about the complex life of these fascinating Social Hymenoptera, I decided to write a short treatise on their life-history and habits. This youthful ambition was interrupted rather suddenly, however, when I was sent to live with some relatives in New York City, and it was not until the summer of 1920, that—due to the acci-

dental discovery of two bumblebee colonies at Berkeley, California—my former interest was again awakened. On June 15 of the following year, I began to make detailed observations on the New England species at the Bussey Institution. The facilities which this school of research and the adjoining Arnold Arboretum offer for the study of bumblebees are probably not surpassed anywhere in the world. On the approximately three hundred acres belonging to these two departments of Harvard University, I have taken thirteen of the seventeen bumblebee species recorded from the New England States. During the past thirteen years there were also discovered more than 250 bumblebee colonies on, or near, the grounds of these two institutions. Of this large number of colonies, representing—if one taken at Petersham, Massachusetts, is included—all but three of the non-parasitic New England species, about 200 were transferred to nest-boxes for further study. In addition, I have made extensive observations on the activities of these industrious insects out in the fields. This work has resulted in the disclosure of many new and significant facts. But before I present these, it seems desirable to say a few words concerning the structure, classification, and distribution of this subdivision of the Social Hymenoptera.

Bumblebees, as their name indicates, belong to the group of insects commonly known as bees (Apidae). As is well known, they obtain their food almost exclusively from flowers, with which, as we shall see, they have entered into an interesting interrelationship. With the exception of several primitive genera and the parasitic species, all bees have well-developed, and in most cases highly modified, organs for collecting nectar and pollen,

and these frequently serve as a means of classification. Using the length of the tongue as a criterion, the Apidae are sometimes divided into long-tongued and short-tongued bees, while their pollen-collecting apparatus has been used in separating them into Podilegidae and Gastri-legidae, depending upon whether they collect pollen on their legs, or on the ventral side of the abdomen. The Podilegidae, the species collecting pollen on their legs, are in turn subdivided into solitary and social bees. To the latter group belong the honeybees (*Apis*), bumblebees (*Bombus*¹ and *Psithyrus*), stingless bees (*Trigona* and *Melipona*), and, as Stöckhert (1923) has recently shown, some, if not all, members of the genus *Halictus*.

Bumblebees, as already indicated, are divided into the two genera, *Bombus* and *Psithyrus*, of which the former comprises the nest-building, the latter, the parasitic species. Although these two genera closely resemble each other, the females of *Psithyrus* can be easily distinguished from those of *Bombus* by the absence of *corbiculae*, or pollen baskets, the outer side of the tibiae of the *Psithyrus* females being convex and hairy, instead of bare and flattened as in *Bombus* (Fig. 1). They differ from the latter also in being less densely clothed with pile, especially on the abdomen, the tip of which, in addition to bearing noticeable ridges on the ventral side, is more pointed and incurved than that of *Bombus*. It is not so easy, however, to separate the males of these two genera. Although the pile of the *Psithyrus* male, like that of the female, is rather sparse, and its tibiae are somewhat more convex and hairy than those of the *Bombus* male, the

¹ In all my previous publications I have used the generic name *Bremus* for the nonparasitic bumblebees. But since it seems probable that the International Commission of Zoological Nomenclature will reject this term, I have decided to retain the name *Bombus* pending the decision of the Commission.

only dependable character for differentiating the males of these two genera is found in the genitalia, the volsella and squama of which are pale and membranous in *Psithyrus*, but brown and corneous in *Bombus*. It may be pointed

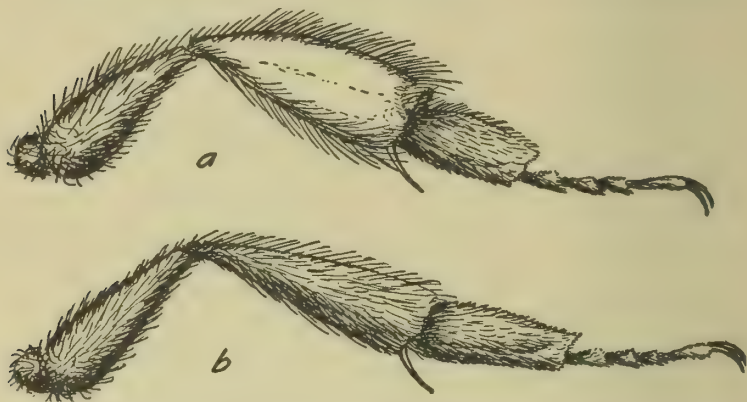


FIG. 1. Hind leg of: *a*, *Bombus affinis*; *b*, *Psithyrus ashtoni*. Lateral view. Greatly enlarged.

out, too, that the *Psithyrus* male usually has a shorter head, and that the pile on its face is predominantly black, while that of the *Bombus* male is almost invariably yellow.

Although one of my friends once showed me two colonies of "bumblebees," which, upon closer investigation, proved to be yellow-jackets, few people have difficulty in distinguishing bumblebees from other insects. The only Hymenoptera with which bumblebees might possibly be confused in this part of North America are *Anthophora* and *Xylocopa*. The latter, *Xylocopa virginica*, superficially resembles the queens of several species of *Bombus*. It can be easily recognized, however, by its deep blue, almost hairless abdomen. The members of the genus *Anthophora*, on the other hand, bear a close resemblance to the workers of certain bumblebee species, but, unlike the latter, they

have a hairless, triangular plate on the dorsal side of the last segment (Fig. 2). However, since I have seen only three specimens of *Xylocopa* during the last thirteen summers, and since *Anthophora*, in addition to being more wary and difficult to catch, is comparatively rare, there is little likelihood of mistaking individuals of these two genera for those of *Bombus* or *Psithyrus*.

Although bumblebees inhabit chiefly the colder regions of the North Temperate Zone, they are also fairly common



FIG. 2. Apical segment of: *a*, *Bombus impatiens*; *b*, *Anthophora floridana*.
Dorsal view. Greatly enlarged.

in almost all of the more mountainous parts of the Tropics, and a few species may be found busily gathering nectar and pollen in the short summers of even such distant regions as Greenland and Alaska, in the Far North, and Tierra del Fuego at the southernmost tip of South America. In the Old World they occur everywhere, except in Australia and the larger part of Africa, where the Sahara Desert seems to prevent them from spreading southward. Originally New Zealand, as well, possessed no bumblebees, but in 1885 several European species were successfully introduced into that country for the purpose of pollinating red clover. One or two species have been taken in the mountains of Borneo, Sumatra, and the Philippines, but in tropical lowlands they are as a rule supplanted by carpenter bees (*Xylocopa*), stingless bees (*Melipona* and

Trigona), and in some cases, by one or more species of wild honeybees. In the New World, bumblebees are universally prevalent, with the possible exception of some of the most northern and southern parts, and a few of the West Indian islands, such as Cuba. While a considerable number of species occur in the plains of both North and South America, they are most numerous along such mountain ranges as the Rockies, the Cascades, and the Sierra Nevadas, as well as in the Andes, where they have been taken at an altitude of almost 14,000 feet. In South America we also find the largest known bumblebee, *Bombus dahlbomii*, a beautiful orange-colored species, the queens of which frequently attain a length of over 30 millimeters.

CHAPTER I

FOUNDING A COLONY

If one takes a walk on a clear, sunny day in middle April, when the first willows are in bloom, one may often see young bumblebee queens eagerly sipping nectar from the catkins. It is a delightful thing to pause and watch these queens, clad in their costumes of rich velvet, their wings not yet torn by the long foraging flights which they will be obliged to take later.

Most of our New England bumblebees are chastely gowned in black and yellow, but if one is fortunate, one may come upon a young queen of the beautiful species *ternarius* (frontispiece), whose orange and yellow pile blends with the colors of the male willow catkins just bursting into blossom. A bit farther on, among the inconspicuous flowers of a female willow, one is almost certain to find a queen of *B. terricola* in her splendid livery of black, banded with yellow. Her fresh, bright colors give no indication that she has but recently emerged from her *hibernaculum* in the soil. Yet this is where many young bumblebee queens spend the winter, a most interesting chapter in the story of their life.

As the season advances, the queens of some species appear in large numbers. Most of them are fond of the early azaleas, and when the buffalo currant (*Ribes aureum*) proffers its golden flagons, one may sometimes see as many as a dozen species on a single bush in the course of an hour. The young *Bombus* queens, however, do not spend all their time in sipping nectar from the flowers, for upon

them rests the responsibility of founding colonies and perpetuating their kind, which, with the exception of these fertile queens, has completely died out during the preceding fall.

The first step in starting a colony is the choice of a nesting-site. This choice varies with the species; some, like *B. fervidus*, *B. americanorum*, and *B. bimaculatus*, prefer to nest on, or near, the surface of the ground, while others, like *B. impatiens*, *B. terricola*, and *B. affinis*, are almost certain to be found nesting in the ground. However, it is apparently by no means an easy thing for the queen to find a suitable place in which to start a colony, and the search, without doubt, sometimes continues for many days, or even for weeks. In the summer of 1924, I saw many young queens of *B. impatiens* and *B. fervidus* seeking nesting-sites as late as July 5. Each species has its own particular method of searching, and an expert can usually tell from a considerable distance to what species a queen belongs, simply by watching her flight for a few moments. The queens of *B. fervidus*, for instance, course swiftly above the ground at a height of about two feet, while those of *B. bimaculatus* fly more leisurely, often settling down, and sometimes anxiously vibrating their wings in a serious absorption in their purpose, as they proceed to inspect a hole or a bunch of dry grass that might prove a favorable spot in which to found a colony. They make a very thorough search. On one occasion I was amazed to see a queen of *B. terricola* enter the silk-lined hole of a large, black spider. Almost instantly, however, she came rushing out, closely pursued by the bloodthirsty owner.

Some of the earlier authors, among them Goedart (1700), Réaumur (1742), and Schmiedeknecht (1878),

PLATE I.



1. A nest of *Bombus impatiens* in an early stage of development, showing honey-pot and clump of brood containing half-grown larvae.
Natural size.



2. Queen of *Bombus impatiens* incubating her brood.
Natural size.

thought it probable that the young bumblebee queen herself digs the underground tunnel leading to her nest, but later observations have shown that this is not true. The young queens of the underground-nesting species often make use of the deserted nest of some rodent, those of *B. affinis*, for example, showing a preference for chipmunk nests, while the surface-nesting species usually select a mouse nest which has been constructed above ground. Although bumblebee queens, as a rule, do not build their own nests, I once observed a queen of *B. muscorum*, one of the European surface-nesting species, gathering bits of dry grass and moss in which she later started a colony.

Bumblebee queens sometimes choose very odd places in which to found a colony. Thus on June 1, 1924, I was surprised to find a young queen of *B. terricola* brooding on the empty frames of a vacant beehive. She was there until June 11, and when the hive was removed, she searched for it frequently on several successive days.

As soon as the queen has selected a nesting-site, she carefully fixes its location in her memory. On leaving the entrance of her future home for the first time, she turns about and surveys it for a few moments, whereupon she slowly rises into the air and describes a series of gradually widening circles, with her head turned toward the place where the nest is situated. This procedure is repeated on subsequent excursions from the nest, but each time the queen describes fewer circles, until at last she leaves and returns to the nest in a comparatively straight line.

Having made a small cavity near the center of the nesting-material, the queen now spends much of her time in the nest, with her body pressed gently against the floor of

the cavity. As a result of the large quantity of nectar which she consumes, a considerable amount of wax exudes from between the segments of her abdomen, according to Hoffer (1882) on the ventral side, as in the case of the honeybee. This has been denied by Sladen (1912), who states that it is secreted only on the dorsal side. My own observations, however, show that it is produced between both the dorsal and the ventral sclerites. When a sufficient quantity of wax has accumulated, the queen constructs a honey-pot near the inner doorway of the nest and fills it with nectar for use during the night, or during inclement weather. The size and structure of the honey-pot vary considerably with different species—that of *B. vagans* has frail, thin walls, while that of *B. separatus* is much more substantially made. In some instances, the queen may even build a double honey-pot, as was the case in an incipient colony of *B. separatus* which I took on June 23, 1924. At the time the nest was taken, this honey-pot was completely closed—an apparently rather uncommon occurrence.

Shortly after the queen has begun to build her honey-pot, she constructs an egg-cell on the floor near the center of the nest-cavity. Judging, however, from the colonies which I reared in artificial nests, the egg-cell may sometimes be constructed first. When the queen is ready to lay, she inserts the tip of her abdomen into the cell, which she then closely embraces with her third pair of legs. As each egg is laid, her sting penetrates the wall of the cell. This led some of the earlier observers to suppose that she had fastened it there as an aid to oviposition.

According to Sladen, the queen builds her first egg-cell on top of a lump of pollen which later serves as food for

the newly hatched larvae. Hoffer, on the other hand, who watched a young queen of *B. lapidarius* start her nest, states that the first egg-cell was built directly on the floor of the nest-box and that the queen shortly afterwards collected pollen which she deposited in the cell. The eggs were then laid in this pollen-primed receptacle. This description agrees with my own observations; but the queens in my nest-boxes, although having pollen available, were not able to collect it from flowers, and probably for this reason, instead of resorting to pollen-priming, fed all of their larvae by regurgitation.

The first batch of eggs, usually about eight in number, hatches in three or four days. As the young larvae grow, swellings appear which indicate their position under the wax covering (Pl. I1). In some species, *e.g.* *B. impatiens*, the queen from time to time opens the waxen envelope, inserts her mouth, and by several sharp contractions of her abdomen injects a yellowish liquid, probably consisting of a mixture of honey and pollen, which is greedily devoured by the larvae. In other species, *e.g.* *B. fervidus*, the worker larvae feed on the pollen that has been deposited directly from the *corbiculae* into one or more waxen pockets constructed at the sides of each batch of larvae. The larvae now grow very rapidly and in about seven days after hatching are ready to spin their cocoons and transform into pupae. During the development of the larvae, the queen has spent most of her time brooding upon the cluster, with her abdomen greatly distended, and her legs grasping the sides of the waxen envelope (Pl. I2). In this manner the cocoons come to lie in such a position that those at the sides are higher than those in the middle, thus forming a groove in which the queen sits while incubating the brood (Pl. II1). This close contact probably

provides warmth for the young, which, although no longer in need of food, are very sensitive to cold. The affection of the queen seems to increase with their development, and she leaves the cocoons only to provide food for herself during the ten to twelve days necessary to complete the transformation from the helpless, maggot-like larva to the full-grown worker bee.

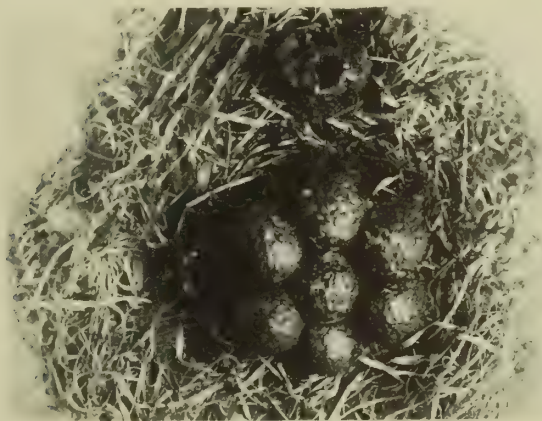
If the brood is chilled, or suffers from lack of food, the duration of the immature stages may be prolonged; but if all goes well, the workers emerge about twenty-two days after the eggs are laid, those in the groove usually hatching a day or so earlier than the others (Pl. IIII). The young workers are as a rule assisted by the queen in cutting their way out of their cocoons, and they in turn lend their aid to those emerging later. The callow, or newly emerged worker, with its silvery gray pile matted against the integument, shows no trace at first of the rich coloring of its mother. After cleaning its legs and antennae, the young worker usually proceeds to the honey-pot, where it takes a deep draught of nectar. In a few hours its coat becomes dry and velvety, and its wings, at first moist and curved closely over the abdomen, become straight, and harden. In two or three days the worker attains its full color, and its wings are now strong enough to carry it on its flights into the field. A worker belonging to an incipient colony of *B. separatus*, which I had under observation, was seen returning to the nest with a load of pollen when but two days old, and I was fiercely attacked by this same individual later in the day.

While her first workers are still in their cocoons, the queen lays several additional batches of eggs. These are usually deposited in cells constructed on both sides of the first clump of cocoons. As the workers one after another

PLATE II.



1. Nest of *Bombus fervidus*, showing the groove in which the queen sits while incubating. Natural size.



2. A nest started by workers of *Bombus fervidus* after they had lost both comb and queen. Under such conditions no groove is formed. Natural size.

leave their cocoons, they share the task of caring for the brood and attend to the foraging, but even now the queen may occasionally take a flight, though most of her time is spent in the nest. Henceforth she lays more frequently, sometimes as often as once a day. The young which hatch from the first-laid eggs are, as a rule, rather small, occasionally only about the size of a bluebottle fly (Pl. III2). As the season progresses, larger and larger workers are produced, until eventually some may be seen which approach the queen in size, so that in certain species, *e.g.* *B. bimaculatus*, it is at times difficult to tell whether one is dealing with a young queen or a large worker. In other species, *e.g.* *B. affinis* and *B. terricola*, the first workers, though showing some variation in size, are as a rule comparatively large; later, the workers of these two species, as well as those of *B. impatiens*, show a uniformity in size almost as pronounced as that of the honeybee.

In the works of several authors, among them Handlirsch (1888), Vogt (1909), and Friese and von Wagner (1910), one not infrequently meets with the statement that all the members of a bumblebee colony are the offspring of one queen, and on this "fact" several of the above-mentioned authors have based far-reaching conclusions in regard to the genetic constitution of certain species. But my own observations, as well as those of Lindhard (1912), Sladen (1912), and Frison (1921), show that queens which have started a colony are often killed and supplanted by others entering their nest; hence, it is possible that the members of a bumblebee colony may be the offspring, not of one, but of several queens. In the vicinity of Boston, this "natural requeening" is especially common in the case of *B. impatiens* and *B. fervidus*. On several occasions I have found as many as eight or ten

dead queens in nests with conspicuous entrances. That it is far from easy, in some cases at least, for such an intruding queen to take charge of a colony, even after its foundress has disappeared, is indicated by the following observation: On June 6, 1927, a queen of *B. impatiens* was introduced into a nest of the same species, from which the original queen had disappeared. The only worker present, although only three days old, immediately attacked the queen and clung tenaciously to her back, with its mandibles fastened at the base of one of her wings. It was finally dislodged, but not until the queen's wings had been torn so severely that she was never again able to fly.

CHAPTER II

THE BUMBLEBEE COLONY IN MIDSUMMER

The comb of a colony examined in midsummer is very different in appearance from the single clump of cocoons and the honey-pot found in nests at the beginning of the season. As already stated, the queen lays additional batches of eggs in waxen cells constructed near the top of the cocoons, and as these develop, and the workers emerge, a comb consisting of several more or less irregular "stories" is built up. The vacated cocoons are smoothed off at the edges and rimmed with wax by the workers, and are then used as receptacles for nectar and, occasionally, for pollen. If more nectar is collected by the colony than is used from day to day, the water from the supply in the cocoons is evaporated, so that the nectar gradually turns into honey, which is much thicker than that of the honeybee. Nectar is stored also in waxen pots which the workers construct, usually at the periphery of the comb, near the entrance of the nest. These pots, however, are never used for making honey; they serve merely as a storage place for the nectar needed by the colony for immediate consumption. In a populous colony, the workers sometimes make as many as a dozen honey-pots in a single day, but these are often torn down later, and the wax is used for other purposes. Hoffer (1883) and Sladen (1912), the two foremost European authorities on the biology of bumblebees, differ as to whether bumblebees cap their honey. The former asserts that this is never the case, while Sladen makes the follow-

ing statement concerning this question: "In a favourable season a populous colony may have all the vacated cocoons, amounting to over 400, filled with thick honey and sealed over with wax." My own observations agree with those of Sladen. In large colonies, especially those of *B. impatiens*, I have repeatedly found a considerable number of the vacated cocoons filled with thick honey, and completely capped, so that no opening could be seen even with the aid of a hand lens.

Some species, such as *B. bimaculatus*, accumulate very little food and live more or less from hand to mouth, while others, more provident, such as *B. affinis* and *B. terricola*, often amass considerable quantities of both honey and pollen. For the storage of the pollen, these species construct long waxen cells, or cylinders, by adding wax to empty cocoons. These cylinders are usually found near the center of the comb and sometimes reach a height of three inches. In a nest of *B. terricola*, taken on July 12, 1923, I found about a dozen of these cylinders which contained more than a quarter of a pound of pollen. Apparently *B. fervidus*, as well, occasionally stores a small quantity of pollen in this way, but the three cylinders which I found in a nest of that species, taken on July 20, 1927, were built on the periphery of the comb. According to Hoffer, only those species which inhabit mountainous regions, where they are often subjected to long periods of inclement weather, have the habit of constructing cylinders for the storage of pollen; but, as we have seen, this assertion is incorrect.

As the colony develops, the comb expands and takes up more and more room in the nest-cavity. It is stated by Wagner (1907) that bumblebees excavate, or at least widen, subterranean cavities for their nests. Sladen, on

PLATE III.



1. Nest of *Bombus impatiens* from which the queen and her first three workers have been removed, showing that the larvae in the groove usually hatch first. Natural size.



2. Incipient colony of *Bombus impatiens*. The young workers which hatch from the first-laid eggs are rather small. Natural size.

the other hand, says: "As the larger and newer cocoons become available for the storage of food, the oldest ones at the bottom of the comb are emptied and used no more, except in a time of plenty, when all the rest are full. In underground nests, where all available space is likely to be needed for the expansion of the comb, the walls of these abandoned cocoons are often bitten down, and the comb sinks. Wasps, it is well known, enlarge their nest cavity according to their requirements by digging out little lumps of earth and flying away with them, but I have never seen humble-bees do this." To this statement, which agrees with my own observations, I may add that the fragments of such dismantled cocoons are often found intermingled with the material with which the bees cover the comb. I have also taken several subterranean nests in which the comb had already filled the nest-cavity and was beginning to grow along the rather wide entrance tunnel.

As the comb increases in size, the bees add to the nesting-material by collecting such substances as moss and dry grass which they may find near the nest—a labor usually performed in the evening, after most of the workers have returned from the field. This activity can as a rule be best observed in the case of the surface-nesting species, such as *B. fervidus*, in a populous colony of which one may sometimes see as many as twenty or thirty workers thus engaged within a foot or two of their home. Facing away from the nest, each worker seizes a bit of moss or dry grass in her mandibles and passes it beneath her body to the third pair of legs, which push the fragment as far as possible in the direction of the nest. A worker nearer to the nest then seizes this material and treats it in the same manner. If the nest happens to be

subterranean, more nesting-material is occasionally gathered by the colony than the nest-cavity can hold. This, then, accumulates over the entrance, forming a "pseudo-nest" in which a number of workers are sometimes found. Such a pseudo-nest may easily be mistaken for a surface nest.

Thus far we have been considering the work of bumblebees in and about the nest; now we come to their more familiar activities in the field. As we have already seen, a flourishing colony of bumblebees consumes considerable quantities of nectar and pollen, the collection of which is one of the most important duties of the workers. It is sometimes asserted that honeybees never forage for nectar and pollen at the same time. This, however, is not true of bumblebees, for they may frequently be observed collecting nectar and pollen simultaneously from red clover. I have also seen workers gathering nectar from vetch, after having filled their *corbiculae* with pollen from other flowers.

✓ The short-tongued species, such as *B. affinis* and *B. terricola*, are unable to obtain the nectar of long-tubed flowers in the normal manner, but they overcome this difficulty by biting a hole near the base of the flower, through which they insert their tongue and obtain the nectar. That this habit is primarily correlated with the length of the tongue, is shown by the fact that the workers of *B. affinis* perforate the flowers of red clover, while the queens of *B. affinis* usually obtain the nectar in the normal way. The habit of perforating the corolla is apparently in the process of becoming a fixed instinct in the case of *B. affinis* and *B. terricola*, since I have on various occasions seen queens and workers of these two species pierce the flowers of rhododendron, from which other queens

and workers of these same species obtained the nectar in the normal manner.

It is also interesting to observe bumblebees collecting pollen. On some plants, such as spirea and small-petaled hydrangea, they merely run quickly over the flowers, but in the case of wild rose and thimbleberry (*Rubus odoratus*), the worker seizes the anthers with her mandibles and first two pairs of legs, and shakes them, emitting an impatient buzz, as if angry because the stamens do not give up their pollen at once. In this connection it might be worth noting that *Anthophora* acts precisely as *Bombus* does when gathering pollen on these flowers, while the honeybee just moves rapidly over the anthers.

When a worker enters the nest on her return from the field, she passes nimbly over the comb in search of a suitable cell in which to deposit her load of nectar or pollen. She is apparently somewhat fastidious in her choice, for she usually examines several cells before she is satisfied. If she has nectar to deposit, she inserts her head into the cell and regurgitates the contents of her honey-sac by several rapid contractions of her abdomen. There has been some difference of opinion as to how a bumblebee deposits her load of pollen. Coville (1890) and Sladen state that this is accomplished by rubbing the posterior legs together. Hoffer, Wagner, and Frison (1917), on the other hand, maintain that the bumblebee removes the pollen with the middle pair of legs. This agrees with my own observations. Frison describes the process as follows: "After the pollen-containing cocoon has been found, the worker stands on the edge, facing away from the cocoon, and inserts her hind legs down into the cocoon; then she proceeds by a quick, slicing, downward movement of the middle pair of legs, to remove the

pollen from the corbícula." It is difficult to conceive how bumblebees could deposit pollen in the manner described by Coville and Sladen; it seems probable, therefore, that these authors overlooked the rapid movement of the second pair of legs.

Although bumblebees collect nectar and pollen from a great variety of plants, each species seems to have its favorite flowers. Thus in spring, when the pea tree (*Caragana*) is in bloom, I have—with rare exceptions—found only the queens of *B. fervidus* visiting it. On the other hand, after thirteen years of observation, I have seen but few individuals of *B. fervidus* on rhododendron and not a single one on mountain laurel—yet both of these plants are favorites with most species of bumblebees.

✓ The honeybee has for centuries been a symbol of industry, but the bumblebee, although this is not generally realized, is fully as industrious as its more famous cousin. If the weather is warm enough, bumblebees usually begin to work on the flowers long before sunrise. Thus on June 22, 1924, workers, carrying large loads of pollen, entered my observation-boxes while it was still fairly dark, and half an hour later I saw hundreds of bumblebees collecting pollen on a small bed of wild roses. On calm, clear days one may sometimes find them working even after sunset, and in the short summers of the Far North they are said to be active among the flowers during almost the entire twenty-four hours.

It has been asserted by several authors, among them Coville and Sladen, that the entire population of a bumblebee colony is at home during the night. At first I, too, was of this opinion, but in the summer of 1921, while taking a colony of *B. bimaculatus*, I noticed that several workers which left the nest after sunset did not return,

although the evening was pleasant and the temperature above 75° Fahrenheit. On the following morning I found these workers, laden with pollen, anxiously searching for their comb at the old nest-site. This observation, which I have since repeatedly made in connection with this and other species, no doubt explains—at least in part—the fact that one sometimes finds considerable numbers of bumblebee workers spending the night on, or near, the flowers of certain plants, such as purple loosestrife (*Lythrum*) and butter-and-eggs (*Linaria*), on which they have been collecting nectar and pollen during the day.

Since the bumblebee worker spends its time in almost ceaseless activity, its life, like that of the worker honeybee, lasts only about a month. Its brilliantly colored pile, at first thick and velvety, gradually wears off in places, especially on the dorsal side of the thorax, and sometimes becomes faded, so that in the case of an old field bee it is often difficult to determine with what species one is dealing. This loss of thoracic pile led Schmiedeknecht (1878) and Hoffer to surmise that the colonies to which such individuals belong have subterranean nests with long entrance tunnels. That this theory is erroneous is shown by the following observations: In a surface nest of *B. fervidus*, which was transferred to a nest-box on July 6, 1921, for observation, the pile of all the members of the colony, including that of the queen, was in perfect condition and remained thus until the latter part of July, when the thorax of all the foraging workers became coated with a layer of pollen, that gradually hardened. The bees were evidently annoyed by this coating of pollen, for they repeatedly tried to rub it off with their middle legs. Whenever they succeeded in doing so, most of the pile on the dorsal side of the thorax came off with the

pollen. Similar observations were made on several *fervidus* colonies during the summer of 1922. Investigation showed that these layers of pollen were acquired by the bees while they were gathering nectar from butter-and-eggs. In view of these facts, it is not surprising that the inferences of Schmiedeknecht and Hoffer in regard to the nesting habits of some of the rarer European species have proved to be wrong.

It is well known that strong colonies of honeybees sometimes rob weaker ones, but I have very rarely found this to occur among bumblebees, even though I kept most of my colonies in adjoining nest-boxes. This raises the question: How close to each other can colonies of bumblebees live, amid a natural environment, without interfering with each other? In this connection, the observations and deductions of Wagner are of interest. A number of years ago he discovered a colony of *B. muscorum*, and about thirty-five centimeters from it, a destroyed bumblebee nest. This led him to conclude that the members of the colony had left the old nest and had built a new one, either because their larvae had been destroyed by parasites, or because they had been robbed of their comb; for bumblebee queens, according to Wagner, never establish their nests in such close proximity. As will be seen from the following observation, this assertion is incorrect. On July 4, 1925, I dug up a colony of *B. fervidus*, consisting of the old queen and about forty workers, whose nest was situated in loose, marshy soil several inches below the surface of the ground. I had just removed the nest and captured the last individual, when I noticed two workers of *B. impatiens* busily carrying away a few blades of dry grass that were left in the nest-cavity. At first I thought I was dealing with a mixed colony, but

a second glance into the nest-cavity and a few taps on the surrounding sod revealed the interesting fact that the cavity also contained a colony of *B. impatiens*, which, it was found later, consisted of the old queen, about twenty-five workers, and a female of *Psithyrus laboriosus*. As indicated by the abundance of brood, both of these colonies were in a flourishing condition, and this despite the fact that their nests had been only three inches apart. However, each colony had its own entrance. No dead bees were found, and there does not seem to be any good reason for assuming that these two colonies could not have lived amicably near each other even if their nests had been contiguous.

In spring, and again in late summer, the bumblebees of New England have a varied assortment of flowers from which to gather nectar and pollen, but from about the middle of July to the middle of August, especially if there is little rainfall, competition is keen, and some of the weaker colonies die out entirely. In 1924, I found little or no brood in most of the colonies taken about the middle of the summer during a period of protracted drought, and the workers that hatched shortly afterwards were much smaller than those produced earlier, no doubt because of insufficient food during the larval stage. Such a period of virtual starvation unquestionably accounts to a large extent for the fact that certain species are very rare in some years and quite common in others. Thus during the period of extremely wet weather from the end of July to the middle of August, 1926, more than a dozen colonies, which I was intending to take, died out completely. It is easy to see, therefore, that the colonies of such species as *B. vagans*, *B. fervidus*, and *B. impatiens*, which produce their young queens and males late in the

season, are in this manner frequently destroyed before they have reared their sexual castes, while others, like *B. bimaculatus* and *B. perplexus*, which complete their life-cycle comparatively early, have already produced their young queens. On the other hand, if the spring is excessively wet and the weather pleasant in summer and autumn, the situation is reversed, and such species as *B. bimaculatus* and *B. perplexus* are likely to be scarce during the following year. This fluctuation in the abundance of certain species is so pronounced that Fries and von Wagner (1910) have even surmised a "Wandertrieb" in the case of some of the rarer European species, but these authors have apparently neglected to take the weather factor into consideration.

CHAPTER III

THE CLIMAX IN THE DEVELOPMENT OF THE COLONY

The ultimate object of a bumblebee colony is not the production of workers, but of queens and males. While some species, *e.g.* *B. bimaculatus*, produce comparatively few individuals belonging to these two castes, a thriving colony of some of the more prolific species, such as *B. impatiens*, sometimes rears from 500 to 1,000.

It was thought by Hoffer (1882) that mating between the young queens and males takes place in the nest, but this is not generally true, as is shown by the extensive observations of Lie-Pettersen (1901), who found young queens and males, especially those of *B. terrestris*, mating in large numbers on the leaves and branches of deciduous trees. It has also been assumed by several authors, notably Wagner (1907), that hybrids frequently occur between various species of bumblebees, but in the course of my work I have found no indications of this.

The males of various species of bumblebees differ widely in their habits. Those of *B. affinis* and *B. terricola*, as well as those of *Ps. ashtoni* and *Ps. laboriosus*, are very sluggish and apparently spend most of their time in sipping nectar from flowers—especially boneset (*Eupatorium*) and wild asters—while those of *B. impatiens* and *B. ternarius* may often be seen flying among patches of goldenrod in search of a mate. Others, such as *B. fervidus* and *B. americanorum*, usually scrutinize the upper parts of each prominent herbaceous plant, as they course

swiftly above the ground. The males of *B. bimaculatus*, on the other hand, may be seen in June and July flying along hedges or rows of bushes, stopping in shady nooks, then swinging away in a half circle, only to repeat the performance a few feet farther on. The behavior of the males of *B. separatus*, however, is by far the most interesting to observe. During the warmest part of the day, I have frequently found one or more males of this species perched on the trunk of a large oak or on the heads of grass stalks in the shade near by, with antennae erect, lying in wait for passing insects and giving chase to the larger ones. If a small stone is thrown into the air within ten feet of them, they, like the kingbird (*Tyrannus tyrannus*) guarding its nest, immediately bound after it and pursue it to the ground. When one of the males flies into the air, the others usually dart after him, and they play about for a few moments, much in the manner of house flies on a warm, sunny day, after which all again return to their former post. So absorbed are these males in their vigilance that they will often crawl upon one's finger and use it as a lookout.

It is a well-known fact that bumblebee workers occasionally take to egg-laying, especially if the old queen is feeble or has disappeared from the nest. Such eggs are generally assumed to produce only males. However, such a keen observer as Hoffer states that large workers, or small queens, as he sometimes calls them, are capable of laying eggs which produce workers, queens, and males. This assertion has been questioned by several authors, but, as will be seen later, there seems to be no good reason for doubting its correctness. Hoffer also reports that he found a young queen of *B. terrestris* which, instead of flying away when the maternal nest was disturbed in

autumn, remained on the comb, shook her wings, and buzzed loudly, as does the old queen under similar conditions. From this behavior he inferred that she had taken charge of the nest; but thus far, it has apparently never been definitely ascertained whether a full-sized young queen ever does take the place of her mother and lay eggs which produce workers, queens, and males. The following observations throw some light on this question. On August 26, 1923, I examined a queenless colony of *B. affinis* in one of my nest-boxes and discovered that one of the young queens in the nest had taken charge of the colony. As a result of this requeening, the colony became completely rejuvenated, for over 100 young workers hatched during the month of September, and in October young queens and males were again produced in the nest. This queen was fully as large as those found in spring, and this, together with the fact that the color pattern of the workers and males of *B. affinis* is quite different from that of the queen, proves conclusively that I was dealing with a queen and not with a large, fertilized worker. On August 27 of the same year, a young queen in another colony of *B. affinis* was likewise found to have taken over the duties of the feeble old queen. Instead of flying away, she, like the queen of the colony examined on the preceding day, defended the nest and tried to pull the nesting-material over the brood which I had uncovered in opening the nest.

According to Hoffer, it is also possible for large workers, or "small queens," not only to lay eggs for all three castes, but also to hibernate and found colonies. For several years I had noticed small individuals of *B. vagans* early in spring, and being interested to determine whether these were fertilized and capable of starting colonies, I captured one and confined her in a nest-box with a full-sized queen

of the same species. Unfortunately, this small female was stung to death before she had laid any eggs. However, on June 9, 1924, I saw what I at first believed to be a worker of *B. vagans* entering a hole in a low bank. I dug up the nest, which contained a honey-pot and seven cocoons, and, to my surprise, discovered that what I had supposed to be a worker was in reality a "queen," for workers hatched from the cocoons, and later more workers, as well as queens and males. There seems to be every reason for supposing that such a female might take charge of the maternal nest, as did the two *affinis* queens, and this was probably the case in some of the colonies which Hoffer had under observation. The appearance of these small, fertilized females early in spring undoubtedly also explains Schmiedeknecht's (1878) belief that "workers" sometimes hibernate and found colonies.

It has been suggested by both Hoffer and Sladen (1912) that young queens may occasionally establish a colony during the summer in which they are reared, but of this I have never found any indications. The question has also been raised by some of the earlier bumblebee students as to whether the young queens forage for the maternal colony in fall. According to my own observations, this very rarely occurs, except in certain species, *e.g.* *B. bimaculatus* and *B. perplexus*, where it not infrequently happens that all the workers have died, while queens are still emerging. Under such conditions, I have on several occasions seen young queens of *B. bimaculatus* collecting nectar and pollen for their younger sisters. Thus, on August 9, 1924, I dug up a nest of this species containing twenty young queens, some of which had but recently emerged, and several queen cocoons which had not yet hatched. A number of the queens were later seen bringing in nectar

and pollen. I found that this was also true of a colony of *B. perplexus*, taken on July 23, 1925, which consisted of nine young queens. In the summer of 1922, I observed an interesting incident in connection with a foraging young queen of *B. bimaculatus* belonging to one of my nest-boxes. A small jelly glass, containing a few drops of diluted honey, had been left on a board on which several colonies of bumblebees were kept. A young queen from a colony of *B. bimaculatus* discovered this honey, which she obtained by crawling down the handle of a spoon that projected from the glass. After she had carried all the honey into the nest, she proceeded to examine the surroundings and discovered several other glasses and some large jars about fifteen feet away. When she found that these were closed, she repeatedly tried to crawl beneath the glass covers. Several times during the next few days, I purposely left a small quantity of honey in a glass tumbler a few feet from the nest-box, and this was invariably secured by the young queen as soon as she had discovered the new supply.

Wagner states that young bumblebee queens take a much longer orientation flight than do the workers, and that *nevertheless*, they have greater difficulty in finding the nest. I have observed the first orientation flight of a large number of young queens and workers belonging to different species, and, although there was considerable individual variation in the aptitude which these bees showed in finding their way back to the nest, I failed to notice any such correlation as that described by Wagner. In fact, if any generalization can be made, the young queens appeared to have less difficulty than the workers in returning to the nest.

This brings up the question of memory in bees. It is asserted by von Buttel-Reepen (1915) and Phillips (1921)

that honeybees lose their memory after they have been anaesthetized, but, as I have recently shown (cf. *American Naturalist*, Vol. 58), this is true of neither honeybees nor bumblebees. In his discussion of memory in the honeybee, Phillips adds that: "If bees are confined for a few days they may be placed in any location and bees wintered in a cellar no longer remember their former locations." Judging from the following observation, however, one can readily see that this question needs further investigation. On September 15, 1923, I dug up a large colony of *B. ternarius* at Petersham, Massachusetts, and transferred it to one of my nest-boxes in Boston, where it was placed on a table out in the open. During the next four weeks this colony produced more than 100 young queens. On May 4—about seven months later—I noticed a *ternarius* queen searching about the table, especially near the spot where the nest-box had stood the preceding fall. She continued this search for about fifteen minutes, and later in the day she, or another *ternarius* queen, was again seen carefully exploring the table. Since bumblebee queens do not ordinarily behave in this manner, there can hardly be any doubt that this was a queen which had been reared in the nest-box, and that she still remembered the place after her seven months of winter sleep.

Another matter about which there has been a difference of opinion is the question as to whether a bumblebee colony that has lost both queen and comb can reestablish itself. Wagner asserts that this is impossible, and that consequently such a colony is unable to contribute anything toward the next generation. Huber (1802), on the other hand, states that bumblebee workers under such conditions have little difficulty in starting a new nest. The discovery of several queenless colonies led me to ques-

tion Wagner's assertion. In order to throw further light on this question, the following experiments were performed during the summer of 1922. On August 1, I removed the entire comb from a queenless colony of *B. fervidus*. The workers, about 100 in number, immediately began to build a new nest and later produced a considerable number of males. Two weeks later I performed a similar experiment with a colony of *B. impatiens*, consisting of about 300 workers, with the same result. More recently I have also taken a queenless colony of *B. fervidus* which clearly shows that it was started by workers (Pl. II2). These experiments and observations prove conclusively that Wagner's contention is incorrect.

As already mentioned, laying workers rarely attack an intruder; instead, they remain on the comb, buzzing excitedly as does the old queen, or a young queen that has taken charge of the maternal colony. They can, as a rule, also be recognized by the shiny and distended appearance of their abdomen. The egg-cells constructed by laying workers are usually smaller than those built by the queen, and the number of eggs deposited is less, two being the most I have ever seen laid at one time by a worker, as compared with the eight or more produced by the queen.

The attitude of the queen toward laying workers is shown by the following observation: On July 17, 1924, I placed a queen of *B. affinis* in a queenless colony of the same species, consisting of about twenty workers, four of which had taken to egg-laying. On the following morning, two of the four were found dead, in all probability killed by the queen, as she continued to be hostile toward the remaining two, but exhibited no animosity toward the other workers.

At about the time when the queen and male eggs are

laid, a very strange scene may occasionally be observed in a bumblebee nest. While the queen is ovipositing, some of the workers crowd about her and attempt to snatch and devour the newly laid eggs. She repels the bolder individuals with legs and mandibles, and sometimes even resorts to her sting. When the queen has finished laying, she closes the cell and usually remains near it for quite a while, guarding it from the workers. I have several times witnessed this interesting, and—from the human standpoint—unnatural behavior in the nests of *B. fervidus*. Somewhat similar quarrels were seen to occur between the laying workers of a queenless colony of *B. impatiens*. The workers would chase each other over the comb, and often while one was engaged in ovipositing, another would push her away from the cell, and then immediately lay her own eggs in it.

The Swiss biologist, Huber, was the first to describe this strange habit, and his observations were later confirmed by Hoffer. About twenty-five years after the publication of Hoffer's work, Wagner, in his treatise on the psychobiology of bumblebees, questioned the accuracy of Hoffer's observations, because Wagner found that whenever he opened an egg-cell in one of his colonies, the workers invariably repaired the damage without molesting the eggs. He therefore concluded that Hoffer had been deceived by the usual excitement among the members of a bumblebee colony when it is exposed to light. It is quite probable, however, that Wagner's (1907) experiments were performed early in the season, when, as I have repeatedly observed, even cells containing newly laid eggs, if opened, are immediately closed again by the workers. Opposed to this negative evidence of Wagner is the additional positive evidence of Lindhard (1912) and Sladen, who state that

this "fight for the eggs" may sometimes be witnessed in the nests of *B. lapidarius*.

We now come to the difficult task of interpreting this curious race-suicidal habit of bumblebees. Huber considers it as an attempt of Nature to restrict the bumblebee population. "The bumblebees," says Huber, "are the largest insects that feed on honey; if their number trebled or quadrupled, other insects would not find any nourishment, and perhaps their species would be destroyed." Sladen suggests that the egg-eating habit is associated with the parasitism of *Psithyrus*. He says: "It is natural to suppose that workers that attempt to devour the eggs of their *Psithyrus* stepmother perpetuate their egg-devouring instinct through their sons that they sometimes succeed in rearing." This explanation does not seem plausible, as I have frequently seen the workers of *B. fervidus* eat their mother's eggs, and this species, as will be pointed out later, evidently does not suffer any members of the genus *Psithyrus* to breed in its nests. The correct solution has apparently not yet been reached, and further and more extensive observations are necessary to throw more light on this interesting phase in the life-history of a bumblebee colony.

The production of the young queens and males marks the climax in the development of the colony. The old queen, if still present in the nest, has lost her former vigor and gradually becomes more feeble, until at last we find her dead or missing. One by one the workers die off, and in a short time the nest is completely deserted. The comb does not long remain intact, for the work of the scavengers has already begun, and the larvae of the wax-moth, *Vitula edmandsii*, and of the beetle *Antherophagus* soon consume the last contents of the nest which once contained a rich and populous colony.

CHAPTER IV

PSITHYRUS, THE "CUCKOO" BUMBLEBEE

The normal course of events in the development of a bumblebee colony is sometimes interrupted by the invasion of a most extraordinary foe, the parasitic bumblebees of the genus *Psithyrus*. These intruders—like the European cuckoo and some of our American cowbirds—perpetuate their kind by laying their eggs in the nests of their more industrious cousins. The latter, like the dupes of the cuckoo, then incubate and rear the young of these lazy guests instead of their own. Before going into detail in regard to this matter, however, it seems desirable to sketch briefly the life-history of these social parasites.

After fertilization, the young *Psithyrus* females, like the young *Bombus* queens, go into hibernation, but leave their winter quarters about a month later than do the *Bombus* queens. Having no apparatus for collecting pollen, the *Psithyrus* female is unable to found a colony of her own, but shortly after leaving her *hibernaculum* she begins to search for a *Bombus* nest. If she succeeds in finding one, and if the colony is in an early stage of development, she is usually able to enter and establish herself without serious interference.

That the *Psithyrus* female does not always gain admittance to a *Bombus* colony without a struggle, is indicated by the frequent discovery in bumblebee nests of dead or disabled *Psithyri* and *Bombi*, and is confirmed by direct observation when a *Psithyrus* first enters, or is placed in, a *Bombus* nest. In these encounters, the *Psi-*

thyryus has a great advantage over the members of the *Bombus* colony, for she has a powerful sting, and her integument is so thick that her opponents are unable to penetrate it with their stings. But, like Siegfried and Achilles, she is vulnerable in certain places, especially the neck, and it is chiefly due to this that she is not always victorious. Thus on June 22, 1923, a female of *Ps. laboriosus* entered one of my nest-boxes containing a colony of *B. terricola*, and in the ensuing battle she and fifteen workers were killed. Two weeks later, this same colony was visited by another *laboriosus* female, and this encounter likewise resulted in the death of the intruder and of more than a dozen workers.

Nevertheless, as already mentioned, a *Psithyrus* female occasionally does succeed in establishing herself in a *Bombus* colony without losing her life and may then remain with the colony until she dies. Here the question arises: What is the attitude of such a *Psithyrus* female and the rightful owners of the nest toward each other? The two foremost European authorities disagree on this point. Hoffer (1889), who studied the habits of the European *Psithyri* more extensively than any other investigator, repeatedly found the *Psithyrus* female living peaceably with the members of the *Bombus* colony, including the host queen. Sladen (1912), on the other hand, asserts that the *Psithyrus* female, at least those of *Ps. rupestris* and *Ps. vestalis*, always kills the *Bombus* queen, either at the time the *Psithyrus* enters the nest, or a few days later, when she is about to begin egg-laying. After the *Psithyrus* has committed this murder, the *Bombus* workers, according to Sladen, constantly watch for an opportunity to avenge their mother by killing the intruder. He vividly describes this phase in the life-history of the *Psithyrus*

female and the afflicted bumblebee colony as follows: "It is the practice of the *Psithyrus* female to enter the nest of the *Bombus*, to sting the queen to death, and then to get the poor workers to rear her young instead of their own brothers and sisters.

"The way in which the *Psithyrus* queen proceeds in order to ensure the success of her atrocious work has all the appearance of a cunning plan, cleverly conceived and carried out by one who not only is a mistress of the crime of murder, but also knows how to commit it at the most advantageous time for herself and her future children, compelling the poor orphans she creates to become her willing slaves. . . . Her first care is to ingratiate herself with the inhabitants, and in this she succeeds so well that the workers soon cease to show any hostility towards her. Even the queen grows accustomed to the presence of the stranger, and her alarm disappears, but it is succeeded by a kind of despondency. Her interest and pleasure in her brood seem less, and so depressed is she that one can fancy she has a presentiment of the fate that awaits her. It is by no means a cheerful family, and the gloom of impending disaster seems to hang over it."

The hostile attitude of the *Bombus* workers toward the *Psithyrus* which had killed their mother—in one case weeks before—is described by Sladen as follows: "It was clear that the workers deposed the *Psithyrus* queen, and I think that this was the culminating act in a revolt that the queen had all along found it difficult to repress. . . . It appears that when the colony is populous the *rupestris* [queen] will lose her life unless she maintains continuously her rule of repression."

Though interesting, this account of the behavior of the *Psithyrus* female and the victimized *Bombus* colony

toward each other conflicts not only with the earlier work of Hoffer, but also with the following observations on the habits of some of our American Psithyri: On August 9, 1921, I dug up a colony of *B. affinis* after much effort, for the tunnel was over seven feet in length. The nest, situated about three feet below the surface of the ground, contained the old queen and nearly 100 workers of *B. affinis*, and the old female, three young females, and six males of *Ps. ashtoni*. The comb consisted of numerous empty *Bombus* and *Psithyrus* cocoons and a large quantity of *Psithyrus* brood in various stages of development. This colony was transferred to a third-story window and kept under observation until September 26. From August 9 until September 14 the nest was examined at least twice a day. Once a week every worker was caught, so that the young Psithyri which had hatched during the preceding week could be collected without incurring the wrath of the colony. The young Psithyri were then placed in a box and fed with honey and pollen until their pile attained its full color. In this way twenty-nine males and sixty-one females of *Ps. ashtoni* were secured, but a considerable number of males, and perhaps a few females, undoubtedly made their escape during the last few days preceding the weekly collections.

Despite the fact that the abdomen of the *Bombus* queen was much distended, and that she was seen to lay eggs on August 10 and subsequent days, not a single *Bombus* queen, male, or worker emerged. As the nights became colder during the early part of September, this *affinis-ashtoni* colony, which by that time had dwindled to about a dozen individuals, gradually died out. On September 12, the old *Psithyrus* female was found dead in the nest, two days later the *Bombus* queen was missing, and the last worker died on September 26.

In this case the *Psithyrus* female must have gained admittance to the *affinis* nest during, or before, the first few days of July. The *Psithyrus* and the *Bombus* queen therefore lived together for at least two months. During the time they were under observation (August 9 to September 12), the two did not show any antagonism whatsoever, nor did any of the other members of this *Bombus-Psithyrus* colony exhibit the slightest sign of hostility toward one another.

On August 10 of the same year, I discovered that a female of *Ps. laboriosus* had gained admittance to a colony of *B. vagans* which had been taken on August 2, and had been transferred to a third-story window of one of the Bussey buildings. At that time, the *vagans* colony consisted of the old queen, about fifty workers, and several males. On the afternoon of the same day, the *Psithyrus* female was observed in the act of tearing open a cell containing small *Bombus* larvae, so that three of them rolled to the bottom of the nest-box, and four others were left exposed. As usual, the larvae were thrown out of the nest a few minutes later by the *Bombus* workers. About 5 P.M., the *Psithyrus* female began to gather wax from the cocoons and built a small cell, in which, about two hours later, she laid several eggs. As each egg was deposited, the sting of the *Psithyrus* penetrated the wall of the cell.

Six of the eggs laid by the *laboriosus* female developed into larvae which spun their cocoons about August 25, and on September 7 a young *laboriosus* female emerged from one of them. The other five cocoons were heavily parasitized by *Melittobia* and did not hatch; nor did any of the *Bombus* eggs develop which were present in the nest when the *Psithyrus* female gained admittance to the colony. Whether or not, in this case, the *Bombus* queen

laid any eggs after the appearance of the *Psithyrus* was not determined.

Except during the first three or four days, the behavior of the *laboriosus* female and of the *vagans* colony toward each other was the same as that of the members of the *affinis-ashtoni* colony. On the first day after the *laboriosus* female entered the nest, she seized nearly every worker with which she came in contact and rolled it toward the ventral side of her abdomen, making movements as if to sting her victim. This mauling lasted only a few seconds, when the worker, which in every case remained passive, was again released. In seizing the workers, both the mandibles and the first pair of legs were usually employed simultaneously, but on one occasion the *Psithyrus* first lifted a worker by the pile of its thorax with her mandibles and then rolled it below her body. None of the workers seemed to be any the worse for this mauling. On the second day, the *Psithyrus* female only occasionally seized a worker and treated it in the manner described. These attacks upon the *Bombus* workers occurred still less frequently on the following day, and thereafter no animosity was noticed between the *Psithyrus* female and the *vagans* workers.

The attitude of the *laboriosus* female and of the *vagans* queen toward one another was somewhat different. From the very beginning the *Psithyrus* paid little or no attention to the *Bombus* queen, but during the first few days the latter avoided the *Psithyrus* whenever they met, and usually turned the tip of her abdomen toward the intruder, as if to ward off an attack. However, these signs of hostility on the part of the *vagans* queen gradually decreased, and after the fourth or fifth day the two lived together in harmony.

To the *vagans* males, of which several were present when the *Psithyrus* first entered the nest, and to two young *vagans* queens which emerged on August 15, the *Psithyrus* paid no attention whatsoever, nor did any of these young queens and males exhibit the slightest sign of fear or hostility toward her.

As in the case of the *affinis-ashtoni* colony, the members of the *vagans-laboriosus* colony became more and more inactive as the weather grew colder. On September 12, the old *vagans* queen disappeared, and four days later the old *Psithyrus* was missing. The two had occupied the same nest for about five weeks.

Similar observations, some of which will be discussed in the following pages, were made on twenty-seven additional *Bombus* colonies in which females of *Ps. ashtoni* or *Ps. laboriosus* were found breeding. Of this total of twenty-nine parasitized colonies, eighteen contained the old *Bombus* queen, while several of the remaining eleven were queenless at the time the *Psithyrus* entered the nest. This clearly shows that *Ps. ashtoni* and *Ps. laboriosus* do not always—if ever—kill the host queen, and in this respect they behave like the two other American *Psithyri* whose hosts are known. One of these, *Ps. insularis*, was found breeding in a colony of *B. flavifrons* by Sladen (1915), and the other, *Ps. variabilis*, has been repeatedly taken in the nests of *B. americanorum* by Frison (1916). In the six infested nests reported by these two authors, each one contained the old *Bombus* queen, and this despite the fact that in several cases young *Psithyri* had emerged, or were about to emerge.

All these observations on the habits of our American *Psithyri* make Sladen's assertion that *Ps. rupestris* and *Ps. vestalis* always kill the host queen appear extremely

doubtful. Sladen's conclusions were based on the fact that he never found a living *Bombus* queen in a *Psithyrus*-infested nest of any of the European species. This negative evidence, as already mentioned, is contradicted by the observations of Hoffer, who found females of *Ps. rupestris* and *Ps. vestalis*, in addition to those of several other European species, living in peace with the host queen. Further inquiry into the queen-killing habit of *Ps. rupestris* and *Ps. vestalis* will in all probability show that Sladen based his conclusions on insufficient evidence.

There still remain several other interesting questions concerning the members of the genus *Psithyrus*, such as origin, oviposition, and similarity in coloration with their host. As regards oviposition, Hoffer, who, despite his extensive observations, never saw a *Psithyrus* oviposit, states that the *Psithyrus* female lays her eggs in pollen masses in which *Bombus* eggs or larvae are already present. This, as previously pointed out, is not true of *Ps. laboriosus*, and, judging from the oviposition of *Bombus*, one would suppose it to be rather improbable of any of the *Psithyri*. The fact that the *Psithyrus* eggs were laid in a separate cell, incidentally also shows that Hoffer's surmise that the *Psithyrus* larvae devour those of their host does not apply to all, if any, members of the genus.

It is further asserted by Hoffer that whenever the old *Psithyrus* female dies while her larvae are still very young, the larvae, as a rule, likewise perish; therefore, he considers it probable that the *Psithyrus* female forages, and—at least during the early larval stages—contributes something to the support of her offspring. But neither of the two *Psithyrus* females which I had under observation in 1921 was ever seen to leave the nest, and, so far as the *ashtoni* female was concerned, foraging was out of the

question, since she was able to fly but a few feet at the time the *affinis-ashtoni* colony was taken. Nevertheless, her brood, including some newly hatched larvae, was in a flourishing condition. This was true also of several other *Psithyrus*-infested colonies which I have since had under observation.

According to Friese (1888), Hoffer, and Sladen, each European species of *Psithyrus* breeds only in the nests of certain *Bombus* species. Some, e.g. *Ps. rupestris* and *Ps. vestalis*, seem to be restricted to a single host, while others, like *Ps. campestris* and *Ps. barbutellus*, have two, and occasionally even more. As regards the thirteen or fourteen species of *Psithyrus* described from the New World, the hosts of only four are known, two having thus far been recorded for *Ps. ashtoni*, two for *Ps. laboriosus*, and one each for *Ps. insularis* and *Ps. variabilis*. But first of all, it seems advisable to define what constitutes a host in order to avoid any misunderstanding. While it is true that some of the European *Psithyri*—e.g. *Ps. rupestris*—breed only in the nests of a particular *Bombus* species, they may nevertheless be found lodging temporarily in those of other species. Therefore, if we wish to avoid confusion, it will be necessary to restrict the term “host” to those *Bombus* species in whose nests a given species of *Psithyrus* is known to breed successfully.

Several authors have raised the question whether or not the members of the genus *Psithyrus* have any workers. Hoffer answers this question in the negative. Among the numerous *ashtoni* females which I have reared, there is so great a variation in size that some specimens are no larger than medium-sized *affinis* workers. If it is true that some of the characteristics which distinguish the queen and the

worker of the Social Hymenoptera are due to a quantitative or qualitative difference in feeding during the larval stage, then the small *Psithyrus* females are comparable to *Bombus* workers. However, as I have discovered during the past few years, they are no more inclined to work than the full-sized females. These small individuals do not seem to be handicapped by their size, for I have seen them searching for bumblebee nests in spring and also found them producing both males and females in the nests of their hosts.

Some of the European *Psithyri*, for example, *Ps. rufipes*, closely resemble their hosts in coloration, while others, like *Ps. campestris*, bear no resemblance whatsoever to their host. This is also true of our North American species. For instance, between *Ps. laboriosus* and its hosts *B. impatiens* and *B. vagans* there is considerable resemblance, especially between the *Psithyrus* male and the host. On the other hand, there is little or no similarity between *Ps. ashtoni* and its two hosts *B. affinis* and *B. terricola*, and between *Ps. variabilis* and its host *B. americanorum*.

Hoffer states that the European *Psithyri* which are parasitic upon *Bombus* species of the same size as themselves, or larger, resemble their hosts more closely than do the *Psithyri* which victimize smaller *Bombus* species. This correlation in size and color between parasite and host may be true of the European *Psithyri*, but it does not hold for our American species. The females of *Ps. ashtoni* and *Ps. variabilis* are both much smaller than the queens of *B. affinis* and *B. americanorum*, and yet, in this case, there is little or no similarity in coloration between parasite and host. The *Ps. laboriosus* female, on the other hand, is somewhat larger than the queen of *B. vagans*; but here,

especially between *Psithyrus* male and host, there is a considerable degree of similarity.

We now come to the interesting question in regard to the origin of the members of the genus *Psithyrus*. Müller (1871), Pérez (1883), Hoffer, Sladen, Lutz (1916), and Wheeler (1919), all of whom have paid more or less attention to this subject, are agreed that the members of the genus *Psithyrus* are a degenerate offshoot from the genus *Bombus*. One of these authors, Pérez, believes that the representatives of the genus *Psithyrus*, because of their "perfect homogeneity," could not have come from several *Bombus* species and, on the basis of structure, tries to show that they have all evolved from a single form which was closely related to *B. mastrucatus*. He also believes that in the course of time *Ps. barbutellus*, *Ps. campestris*, and *Ps. vestalis* became more differentiated from this original type than did the other *Psithyrus* species. Hoffer and Sladen, however, maintain that there is no evidence for such an assumption, and it is further suggested by Sladen that resemblances, such as coat color, between the various species of *Psithyrus* and their *Bombus* hosts are "clearly attributable to mimicry or exposure to the same conditions of life, and not to ancestry." If we accept this explanation, it is difficult to account for those cases where there is not the slightest similarity between *Psithyrus* and host.

Just how the parasitic habits of *Psithyrus* may have originated is suggested by some observations of Sladen. According to this author, many of the later appearing queens of certain *Bombus* species do not take the trouble to start colonies, but enter nests already occupied by their own or other species. In the resulting conflict the foundress of the colony is sometimes killed, and her offspring

then assist in rearing the brood of the intruder. He states that this occurs frequently between the queens of *B. terrestris* and its smaller relative *B. lucorum*, the latter serving as a temporary host. From this temporary social parasitism, as he points out, it is but a step to the permanent social parasitism of the members of the genus *Psithyrus*.

In the vicinity of Boston, I have found that a similar relationship exists between two of our New England species. During the past thirteen years, I have taken a number of *affinis* nests containing one or more workers of *B. terricola* and, in some cases, even a dead *terricola* queen. It is evident, therefore, that these colonies were founded by a *terricola* queen which was later supplanted by a queen of *B. affinis*. In this connection it seems worth noting that, as in the case of *B. terrestris* and *B. lucorum*, the temporary host likewise is smaller than its "parasite" and appears earlier in the spring.

CHAPTER V

ADDITIONAL OBSERVATIONS ON PSITHYRUS

The *Psithyrus* female, as we have seen, leads a quiet and peaceful life after she has once succeeded in establishing herself in the home of her host. But it is no less difficult for her to find a nest of the particular species which she parasitizes than it is for a *Bombus* queen to discover a suitable place in which to start a colony. In her search for a breeding place, the *Psithyrus* female not infrequently gets into the nests of species other than her host. In some of these, as we shall see, she is received in an indifferent, if not friendly, manner, but in others, as already pointed out, the owners of the nest do not allow her to enter, even at the cost of their own lives.

The question has sometimes been raised as to how the *Psithyrus* female finds a colony of her host. According to Sladen (1912), she is largely guided by scent, and is much more likely to find the nest if it has a short tunnel. In support of this view, he points out that most of the *Psithyrus*-infested nests which he dug up had tunnels not exceeding fifteen inches in length, and never more than two feet long. He therefore considers it probable that species like *B. lapidarius* and *B. terrestris* often have longer tunnels than other species in order to escape being parasitized. A similar opinion is held by Wagner (1907), who, during the summer of 1905, discovered several nests of *B. muscorum* at some distance above ground, and concluded that the nest-building instinct of this species, which normally builds on the ground, is in process of

transformation. The cause for this change he ascribes to natural selection, since, according to this author, the colonies of *B. muscorum* are destroyed in large numbers by various species of *Psithyrus*. That these precautions are not an absolute insurance against the invasion of *Psithyrus*, at least in the case of some of our American species, is shown not only by the fact that I have taken a considerable number of nests of *B. affinis* and *B. impatiens* which were parasitized by *Ps. ashteni* or *Ps. laboriosus*, even though they had tunnels ranging from five to ten feet in length, but also by the frequent appearance of *Psithyrus* females in *Bombus* colonies which I kept in a third-story window, about thirty feet above the ground. Since *Psithyrus* females had succeeded in finding these nests, I at first was led to believe that these parasites had an even keener olfactory sense than was assumed by Wagner and Sladen. This conjecture seemed to be corroborated by the following incident:

On July 3, 1921, a colony of *B. bimaculatus* was dug up. The comb had hardly been exposed when a *laboriosus* female swooped down upon it. She was captured, and, half a minute later, another was buzzing about the nest. This one, too, was caught, but within another minute a third *laboriosus* female alighted on the comb. However, the following observations and experiments, made since that time, have convinced me that these three *laboriosus* females were probably attracted to the nest-site of this *bimaculatus* colony by stimuli other than that of odor.

On July 3, 1924, I dug up a nest of *B. bimaculatus* which had several conspicuous entrances. Shortly after removing the comb, I noticed three females of *Ps. laboriosus* searching near the nest-site, and entering various holes in its vicinity. After they had spent a considerable

time in this manner, two of the females flew away, and I then placed the comb on some newly mown grass directly over the nest-cavity. After a minute or so, the remaining *laboriosus* female alighted about three inches from the comb, but instead of approaching it, she crawled under the grass. Several minutes later, she reappeared about an inch from the comb, and this time found it without difficulty. I then drove her away, and placed the comb about twenty feet from the old nest-site. Although several females of *Ps. laboriosus* were seen eagerly searching about the place during the next thirty minutes, none approached the comb. The experiment was then discontinued, but was resumed at 10:30 A.M. on the following day, when the comb was again placed directly over the old nest-site. At 10:42 A.M. a *laboriosus* female appeared, and crawled into several holes near by. In flying from one hole to another, she came within about two inches of the comb, but failed to notice it, and finally flew away. These experiments clearly indicate that the olfactory sense of *Psithyrus* is not as keen as is generally assumed; in fact, it is questionable whether it is any keener than that of *Bombus*. Yet the sudden appearance of the three *laboriosus* females near the two *bimaculatus* nests referred to still remains to be explained.

As early as the summer of 1921, I had noticed that females of *Ps. laboriosus* often appeared in the nests of my *bimaculatus* colonies and sometimes remained for several days without any serious objections on the part of the owners. In taking colonies of this species, I have also repeatedly found a *laboriosus* female lodging in the nest, but since *Ps. laboriosus* apparently never breeds in the nests of *B. bimaculatus*, I have come to the conclusion that not infrequently one or more *laboriosus* females may

know the location of a nest of this species, and use it merely as a kind of hotel. That this—and not a keen olfactory sense—is probably the correct explanation for the frequent appearance of *laboriosus* females while colonies of *B. bimaculatus* are being taken, is indirectly confirmed by the fact that not a single *Psithyrus* has ever appeared during the process of transferring nearly 175 nests belonging to other species.

Just how two females of *Ps. laboriosus* behave toward one another when they meet in a *bimaculatus* colony, is shown by the following observations: On July 4, 1924, I noticed that a *laboriosus* female was trying to enter through the wire screen at the side of a nest-box containing a colony of *B. bimaculatus*. After several futile attempts, she finally succeeded in finding the flight-hole. A few minutes later, another *laboriosus* female appeared, and flew directly to the entrance of the nest-box. Being interested to know how these two visitors would react toward each other, I removed part of the nesting-material in order to see what would happen. As soon as the second *Psithyrus* female noticed the one which had entered first, she attacked her forthwith, but the one assaulted tore herself loose and hurriedly made her escape through the flight-hole.

Very different from the attitude of *B. bimaculatus* is that of *B. impatiens* when a *Psithyrus* female enters, or is placed in the nest. What occurs in this case is illustrated by several experiments which I performed by putting a female of *Ps. laboriosus* or *Ps. ashtoni* in a large colony of this species. As soon as the parasite was introduced, a great uproar arose in the colony. The workers rushed madly in every direction, searching for the source of the disturbance. The *Psithyrus* was seized almost

immediately by numerous workers which tried to sting her, and was thus rendered virtually helpless. A few bellicose workers, unable to get at the intruder, fastened themselves with their mandibles to some of their fellows in the struggling mass, and attempted to sting toward the center. On one occasion, such a fighting mass was lifted out of the nest-box with a pair of forceps, and when the workers finally released their hold, it was found that the ball had consisted of the *Psithyrus* and seventeen workers. The *Psithyrus* and four of the workers had been severely stung and died within a short time. Although the *Psithyrus* female made vigorous attempts during the struggle to sting her adversaries, she may not have been responsible for any of the deaths, for it was noticed that one of the four workers was killed by another worker at the periphery of the mass, and it is possible that the other three may have met death in the same way. At the beginning of one of these experiments, two workers in their excitement attacked each other several inches from the *Psithyrus*, and one was mortally stung. These experiments with colonies of *B. impatiens* invariably resulted in the death of the *Psithyrus*.

The following incident, however, shows that a battle between a *Psithyrus* female and the workers of *B. impatiens* may end quite differently under somewhat different conditions. On July 24, 1921, nineteen workers of a colony of this species, which had been transferred to one of the Bussey buildings on the preceding day, were caught at the old nest-site and placed in a glass jar. A few minutes later, a female of *Ps. laboriosus* was discovered on some comb which had been left in the empty nest-cavity of a colony of *B. fervidus*. Just to see what would happen, the *laboriosus* female was also placed in the jar. All the in-

mates, including the *Psithyrus*, were ill at ease, and tried to escape, but one or two of the workers nevertheless attacked the *laboriosus* female as soon as they came in contact with her. The latter now went on the warpath herself. She quickly seized one worker after another, whether attacked by them or not, rolled them below her abdomen and stung them to death. This done, she seemed to feel quite at home in the jar, and began to lap up the honey which was oozing from the bodies of her victims. Incidentally, this experiment also shows the incorrectness of Sladen's conclusion that workers mauled by a *Psithyrus* female are not injured because they are too small.

How different the behavior of two species of *Psithyrus* may be toward a *Bombus* colony is shown by the following experiments: On June 25, 1926, a female of *Ps. ashtoni* was captured in the field and placed in a jar containing a considerable number of workers and five young queens of *B. bimaculatus*, as well as a female of *Ps. laboriosus*. On my journey home, the *ashtoni* female killed the five young *bimaculatus* queens and more than a dozen workers, but did not attack the *laboriosus* female. However, when about a week later a female of *Ps. laboriosus* was caught out in the open and put in a jar with a fair-sized colony of *B. bimaculatus*, there was not the slightest indication of any hostility.

From 1922 to 1928, I kept several colonies of honeybees in connection with my work on bumblebees and often found dead, or paralyzed, females of *Ps. laboriosus* in front of my hives. These dead, or dying, bees were usually more or less denuded of pile, and in a few cases the antennae, wings, and tarsi were badly mutilated. I have also frequently noticed that the females of this *Psithyrus*, and occasionally a queen or worker of some of

the nonparasitic bumblebees, make determined attempts to enter the hives, even after they have been repeatedly repelled by the guards. These observations led me to conclude that the *Psithyrus* females had attempted to gain admittance to the hives, and that the guards had summarily "executed" them, without any serious sacrifice on their part. But as will be seen from the following incident, I was mistaken in the last part of my assumption.

In the early afternoon of July 2, 1925, I visited my two hives, No. 1 containing a medium-sized colony of three-banded Italians, and No. 2, a strong colony of Carniolans. I noticed several workers, with their abdomens curved below the body, hurriedly crawling out of the entrance of hive No. 2. From previous observations I knew that these individuals had been stung. This led me to suspect that the colony was giving battle to a *Psithyrus*, a surmise corroborated a few seconds later, when a female of *Ps. laboriosus*, with about a dozen workers of *Apis mellifica* clinging to her legs, antennae, and wings, came creeping slowly out of the entrance. In trying to throw off her enemies, the *Psithyrus* lost her footing, and more bees joined the fray as she began to struggle with her assailants. As in the case of *B. impatiens*, those workers which were unable to get at the intruder, seized one of the workers clinging to the *Psithyrus*, and in this way a ball, about two inches in diameter, was formed. After a few seconds the ball fell from the entrance to the ground, and the resulting jar caused many of the bees to release their hold. But a considerable number refused to let go of the intruder until a few minutes later, when the *Psithyrus* female had become so paralyzed that she was no longer able to crawl. Four of her adversaries were likewise completely disabled,

while about a dozen others were only partially paralyzed. Several of these were placed in a box, but all died within a short time.

Sladen believes that *Psithyrus* females never kill one another, because he never found a dead *Psithyrus* in a *Bombus* nest ruled by a *Psithyrus*. This is certainly not true of *Ps. laboriosus*. During June, July, and August, females of this species are usually very common in the vicinity of Boston, so that numerous experiments along this line could be carried out. At various times *laboriosus* females were caught out in the field, and placed in a small box containing comb filled with honey. Whenever two such females were put into this receptacle, or a similar one without comb, they immediately engaged in a violent battle, which almost invariably resulted in the death of one of the combatants.

Females of *Ps. laboriosus* that were searching for bumblebee nests were also frequently placed in *bimaculatus* colonies in which a *laboriosus* female was already present. The two *Psithyrus* females usually attacked each other at once, and within a minute or two, sometimes even within a few seconds, one toppled over, mortally stung. Occasionally the second *Psithyrus* female tried to avoid a conflict by making a dash for the flight-hole as soon as she noticed the other *Psithyrus*. But if both females were in a pugnacious mood, they generally seized each other by one of the legs and endeavored to use their stings. As soon as one had succeeded in accomplishing this, she attempted to extricate herself from the embrace of her vanquished foe. During these encounters it sometimes happened that legs were torn off, or that the dead *Psithyrus* had fastened her mandibles so firmly to one of the legs of the victor that the latter had to be released. Such a *Psithyrus* in turn was

not infrequently killed a few minutes later by a third Psithyrus that was introduced into the nest.

Although the Psithyrus female is a valiant warrior and sometimes victorious even against considerable odds, she is apparently unable to cope with *B. fervidus*, from whose nests, as we shall see later, she is expelled by a subtle, but most effective, method.

CHAPTER VI

COMMENSALS, PARASITES, AND PREDATORS

While *Psithyrus* is the most dramatic disturber of the peaceful life of a bumblebee colony, this foe is by no means the most destructive, for the nest not infrequently harbors various intruders, some of which merely act as scavengers, while others are deadly parasites of the brood (Pl. IV₁). In addition to these harmful denizens of the nest, there are also enemies which attack the adult bees in the field, or rob them of their brood, or of their stores of honey and pollen.

Among the scavengers occurring in bumblebee nests, the larvae of *Diptera*, *Coleoptera*, and *Lepidoptera* are the most common. To the first of these three orders belong the larvae of *Volucella*, a large fly, whose color patterns resemble those of certain species of bumblebees. It has been suggested by Gabrichevski (1924) that such mimicry is useful to the female when she enters a *Bombus* nest to lay her eggs, but this conjecture seems doubtful, since I have found the larvae breeding in the nests of *B. fervidus*, a species not approached in coloration by any American *Volucella*. It is probable, however, that the members of this genus derive considerable protection from various enemies because of their striking resemblance to their host. The adult flies are often seen on flowers frequented by bumblebees, and, when caught, emit a similar buzz. Their flight, too, is similar, and at a distance of ten or twenty feet a *Volucella* might easily be mistaken for a bumblebee male or worker. According to Gabrichevski,

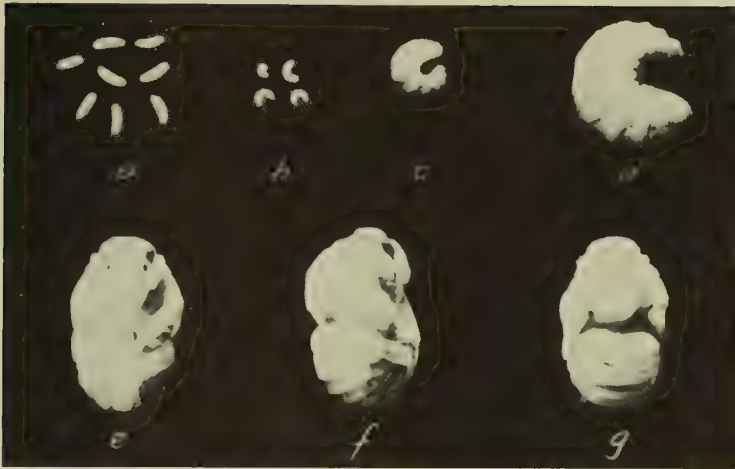
who has made extensive observations on *Volucella* in Europe, the behavior of these flies in the nest is also much like that of their host. This author found that if a female is placed in an observation-box with a number of bumblebees, and tickled with a straw, she raises one of her middle legs and buzzes loudly—in other words, she acts precisely as a bumblebee does under these conditions.

Several authors, among them Schmiedeknecht (1878) and Hoffer (1882), state that the larvae of *Volucella* attack and eat the brood of their host. Sladen (1912) and Gabrichevski (1926), on the other hand, assert that these larvae never harm the brood, a statement which is corroborated by my own observations both in this country and in Europe. Although twenty-two full-grown *Volucella* larvae were present in a nest of *B. fervidus* which I took in the summer of 1921, the brood was in a flourishing condition, and showed no signs of having been injured in any way. Since I have invariably found the larvae of the fly below the deserted cocoons, it seems reasonable to assume that they feed chiefly upon the débris at the bottom of the nest.

The larvae of *Fannia*, another dipterous insect, are also sometimes met with in bumblebee nests, especially if the latter are situated in damp soil. On several occasions I have found a large number of them in the nesting-material below the comb, as well as in the soil beneath the nest. These larvae are much more sluggish than those of *Volucella*, and can be distinguished by the presence of several rows of prominent spines (Pl. IV₂) along their entire length, instead of only a few at the anal end, as in *Volucella*.

One of the most interesting scavengers, the adults and larvae of which occur in practically every bumblebee nest,

PLATE IV.



1. Immature stages of *Bombus americanorum*: a, eggs; b, c, and d, larvae; e, f, and g, pupae. Somewhat enlarged.



2. Larvae of, a, *Antherophagus*; b, *Vitula edmandsii*; c, an undetermined hymenopterous parasite; d, *Fannia*; e, *Brachycoma sarcophagina*. Slightly enlarged.

is the beetle *Antherophagus*. According to Wagner (1907), its larvae cause enormous destruction, but I have never found any evidence of this, although I have repeatedly seen several hundred larvae (Pl. IV2a) in all stages of development in a single nest.

Antherophagus has a novel way of gaining admittance to a bumblebee colony. The adults frequent flowers, such as hydrangea and hollyhock, where I have seen them lying in wait with wide-open mandibles. When a bumblebee approaches, they seize it by its tongue, or by one of its legs or antennae, and are thus carried into the nest. Here, as I have often observed, the adults mate, and the female then lays her eggs, very likely in the deserted cocoons, or in the débris beneath the comb.

How long these beetles sometimes cling to their porters is shown by the following observations: While taking a surface nest of *B. fervidus* during the summer of 1921, I noticed an *Antherophagus* attached to a hind leg of one of the workers. About fifteen minutes elapsed before the worker was captured, and during all this time the beetle retained its grip. On several occasions I have seen an adult *Antherophagus*—and in one case even two—attached to the appendages of a worker of *B. impatiens* while the latter was foraging on hydrangea and *Eupatorium*. As will be seen from the accompanying illustration (Pl. V2), these beetles may cling so tenaciously to their host that they do not release their hold even after being placed in a cyanide jar.

According to Hoffer and Sladen, the larvae of the large wax-moth, *Aphomia sociella*, cause considerable damage in the nests of European bumblebees, not only destroying their comb, but also feeding upon the brood. This moth apparently does not occur in the United States, but

a smaller and comparatively harmless species, *Vitula edmandsii*, is quite common in New England, where I have found it breeding in large numbers in surface nests. The larvae (Pl. IV2*b*) of this moth usually do not appear until late fall, and feed upon the old comb and refuse in the then partly or wholly deserted bumblebee nests. I have frequently seen hundreds of these larvae hibernating in and below a single nest-box. In a few nests which were transferred to the laboratory in the fall, the larvae started to pupate in November. The adults began to emerge during the first week of December, and continued to hatch until the latter part of March. A large percentage of these larvae and pupae were parasitized by a small braconid wasp of the genus *Habrobracon*.

I have also found the pseudo-scorpion *Chelanops sanborni* Hagen in the nesting-material of several subterranean colonies, but did not determine on what it subsists. Professor Nathan Banks, of Harvard University, informs me that he has frequently seen *Chelanops sanborni* attached to the appendages of various insects; hence it is probable that these pseudo-scorpions, like *Antherophagus*, get into bumblebee nests by phoresy.

Ants likewise sometimes enter bumblebee nests, and while it is possible that some of the less audacious species, such as the thief ant, *Solenopsis molesta* Say, merely feed on refuse, other more aggressive species invade the nest for the purpose of stealing honey. During the summer of 1921, ants molested my colonies so frequently that I was obliged to resort to birdlime to keep them out, for bumblebees are apparently unable to combat these thieves. On several occasions I have also seen a bumblebee worker out in the open making frantic attempts to rid itself of an ant which was firmly clinging to one of its antennae.

We now come to a group of intruders some of which affect the welfare of a bumblebee colony more seriously than do those we have thus far considered. This group includes several deadly entoparasites, and a comparatively harmless ectoparasite, the mite *Parasitus bomborum*. Both the nymphs and the adults of this small brown mite are to be found crawling over the comb in almost every bumblebee nest, and occasionally are present under the waxen envelope enclosing the larvae. They probably hibernate on the young queens, for the latter are sometimes almost covered with them in spring, so that, even at a short distance, it is often difficult to tell to what species such queens belong. The food of these mites has apparently not yet been determined, but it seems likely that they live, at least in part, on the exudates of the larvae and adult bees.

Among the internal parasites which attack the brood of bumblebees are the larvae of *Brachycoma* (Pl. IV2e), a tachinid fly closely resembling the house fly. I have found a considerable number of colonies, especially those of *B. fervidus* and *B. bimaculatus*, completely destroyed by the larvae of this parasite. According to Frison (1926), the eggs or larvae are deposited on, or in, the cells containing bumblebee larvae. Parasitized larvae sometimes proceed far enough in their development to spin a thin web of silk about themselves. Such cocoons can easily be recognized by their watery appearance, and—if a colony is heavily parasitized—by a characteristic, disagreeable odor. On several occasions when I have opened cocoons containing parasitized pupae, one or more *Brachycoma* larvae came quickly out of the aperture and crawled into the nesting-material. Although these parasites are no doubt sometimes liberated by the workers, I have ob-

served that they are able to escape from their prison without assistance. Upon leaving the cocoon, the full-grown *Brachycoma* larvae usually attach themselves to the nesting-material, where they pupate.

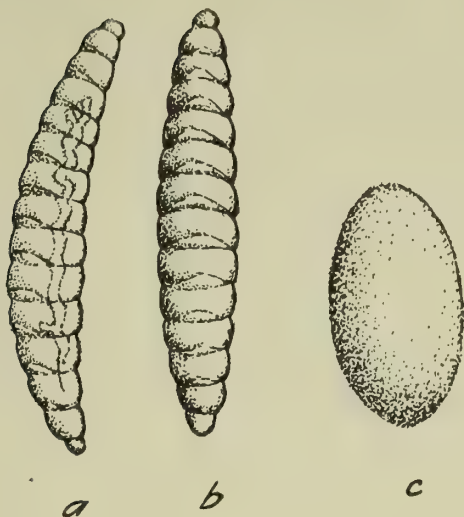
Bumblebee brood quite frequently also falls prey to the larvae of the small parasitic wasp *Melittobia*. The eggs of this parasite are probably laid in cells containing full grown larvae, or young pupae, and the adults later cut their way out of the cocoons. Professor C. R. Kellogg, to whom I turned over a number of parasitized pupae, reared over 100 adults of *Melittobia* from a single queen cocoon of *B. affinis*.

Among the more important internal parasites which attack adult bumblebees are the conopid fly, *Physocephala tibialis*, and the nematode worm, *Spherularia bombi*. The latter apparently parasitizes only queens, in whose bodies it is said to over-winter. This nematode is very prolific. It has been estimated that over 100,000 young worms are sometimes produced in the body of a single queen. *Spherularia bombi* has long been known in Europe (cf. Sladen, 1912), and in this country it has been reported by Dimmock (1886) and Frison (1926b).

While *Spherularia bombi* has thus far been reported as occurring only in queens, *Physocephala tibialis* seems to victimize chiefly workers. I have found a larva or a pupa of this fly in the abdomen of numerous dead workers of various species. Ailing bumblebee workers may often be seen on flowers in late summer. If they are dissected, one not infrequently finds a larva of *Physocephala tibialis* in their abdomen.

According to Hoffer, Sladen, and Friese (1923), the larvae of a European conopid also parasitize the bumblebee brood, the flies emerging from the adult bees, some-

PLATE V.



1. Larvae and cocoon of an undetermined hymenopterous parasite of bumblebee queens: a, larva, lateral view; b, dorsal view, and c, cocoon. About fifteen times natural size.



2. Antherophagus clinging to the tongue of a worker of *Bombus vagans*. After Wheeler.
Greatly enlarged.

times even after the latter have been placed in a collection. However, as is indicated by the following observations, these authors are probably mistaken in regard to the first part of their assertion. On July 5, 1927, I saw a female of *Physocephala tibialis* pounce upon a worker of *B. bimaculatus* while the latter was gathering nectar from vetch. Either as a result of the impact, or because the worker was startled, it fell to the ground, whereupon the conopid released her hold and flew away. Soon afterwards, I noticed the same or another conopid sitting on a leaf, evidently awaiting a chance to swoop down upon an unsuspecting victim. When a bumblebee worker approached, she suddenly darted toward it and seized it, and a few moments later treated another one in the same manner.

In addition to the enemies discussed above, I should like to call attention to an apparently unrecorded, hymenopterous parasite. On June 7, 1923, I liberated an ailing queen of *B. ternarius* which I had been using in breeding experiments. The abdomen of this queen was much distended, and she walked slowly and with difficulty. After she had been released, I noticed a number of small larvae, about five millimeters long and one millimeter in diameter (Pls. IV_{2c} and VI), on a tin can in the nest-box where she had been confined. Two days later, several more of these larvae were found in the nest-box of another queen of *B. ternarius*, which seemed to be suffering from the same malady. On dissecting her, I found nearly a hundred of these small larvae in her abdomen. On the next day, a queen of *B. bimaculatus* was captured, and, shortly after confining her, I noticed that she, too, showed these symptoms, and that a number of the parasitic larvae were present in the nest-box. She was then placed in a glass jar and provided with food, but was

dead on the following morning. A considerable number of larvae were found in her abdomen, and a few more were in the jar. About half of these larvae were placed in some dry sand, where they shortly afterwards spun their cocoons (Pl. VI). Unfortunately, however, no adults emerged, probably because the environment was unsuitable.

Among the more important foes that prey upon bumblebees in the field are the robber flies (asilids) of the genus *Dasyllis*, two species of which, *grossa* and *thoracica*, are common in the vicinity of Boston. *Grossa*, the larger of these, is about the size of a bumblebee queen, and bears a striking resemblance to the female of *Psithyrus laboriosus* (Pl. VIc). One day I was watching a *grossa* female sitting on a leaf of a small shrub, when a queen of *B. fervidus* flew past. The fly immediately darted toward the queen, but stopped suddenly when about two inches from her and returned to the leaf, where she was captured and placed in a jar. The *fervidus* queen alighted a few feet away, and was also captured and confined in the jar. The two insects fought for a long time, until the fly suddenly fell on her back and remained completely motionless. Believing she had been stung, I shook out both insects. The *fervidus* queen flew away at once, and a second or two later, the fly—having merely feigned death—bounded into the air and disappeared. However, these flies do catch and destroy bumblebees, as is shown by the following incidents: On July 23, 1924, I saw a female of *Dasyllis grossa* pounce upon and carry off a worker of *B. fervidus*, while the latter was collecting nectar from *Baptisia*. I saw another fly of this species feeding upon a bumblebee on August 3, 1927, and on catching her I found that her victim was a male of *B. perplexus*. It may be noted that in

both cases the color pattern of the prey was quite different from that of the asilid.

Dasyllis thoracica, the second of these flies, is about the size of a bumblebee male or worker, and, like *grossa*, resembles *B. impatiens* in coloration. Although I have never seen flies of this species attack bumblebees, it is probable that they do not differ from *grossa* in that respect.

Spiders, as is well known, prey on various insects, and bumblebees, despite their sting, are not immune. In the vicinity of Boston I have found chiefly two species, *Argiope aurantia* and *Misumena vatia*, feeding upon bumblebees. The first of these captures its victims by means of a strong web, while the second lies in wait on various flowers, where I have frequently come upon one or more individuals, each with a bumblebee dangling from its fangs (Pl. VII).

Bumblebees, no doubt, occasionally also fall prey to insect-eating birds. I have frequently watched parents and young of the kingbird (*Tyrannus tyrannus*) perched on a fence near my hives, snapping up every honeybee that came their way, and it is probable that this bird sometimes devours bumblebees as well. Hoffer tells of a shrike that swooped down upon pinned specimens which he had drying out of doors, seized one of the bumblebees, pin and all, and flew away with it. Crows, too, have been accused of eating bumblebees and their brood, a charge which seems to be confirmed by the following observation: On June 28, 1923, I discovered a surface nest of *B. fervidus* in a newly mown field where several crows were feeding. When I returned later in the day to take the nest, the comb was gone, and near the nest-site were found about a dozen dead workers which bore evidence of having been killed by the beak of a bird.

Undoubtedly incipient bumblebee nests are sometimes destroyed by field mice and other rodents, while the queen is away foraging. That skunks not infrequently are responsible for the sudden disappearance of bumblebee colonies is shown by some observations which I made during the summer of 1923. At that time I had about sixty *Bombus* colonies, of which all but one were in places where they could not be molested by ants, the single exception being a colony of *B. fervidus*, that was kept beneath a table out in the open. On the morning of August 21, I discovered that the nest-box of this colony was entirely empty, except for some sawdust, a few shreds of cotton, and about half a dozen workers which were frantically searching for their brood. For the benefit of these five or six workers, another *fervidus* colony, consisting of a queen and about thirty workers, was transferred to the spot. Three days later, however, I found that this colony, too, had been completely destroyed during the night. I therefore decided to ascertain the identity of the marauder, and in the evening set a trap baited with bumblebee comb. To my great satisfaction, a half-grown skunk was in the trap on the following morning. Being interested to know how this animal is able to dispose of a whole bumblebee colony, apparently without being stung, I decided to keep it, to see whether I could not make some observations on its bee-eating habits.

For this purpose, the skunk was provided with a special domicile, composed of two adjoining boxes, each measuring about $2 \times 2 \times 2$ feet, one of which may be called compartment No. 1, and the other, compartment No. 2. Compartment No. 1 was partly filled with hay and kept completely closed, except for a small opening (about 6×9 inches), communicating with compartment No. 2,



a



b



c



d

PLATE VI

Bumblebees mimicked by flies. *a*, worker of *Bombus ternarius* and *b*, its mimic, *Eristalis flavipes*. *c*, female of *Psithyrus laboriosus* and *d*, its mimic, *Dasylis grossa*.

About natural size.

while the latter was provided with a layer of sand and sawdust and a wide-meshed wire cover. In this way I was able to supply the skunk with food, without running much risk of being sprayed, for he habitually spent the day in compartment No. 1 and prowled about in compartment No. 2 at night.

On August 27, a colony of *B. fervidus*, consisting of a queen, about fifty workers, and some brood, was placed in compartment No. 2 shortly after dark. I waited until about 9 P.M., but the animal refused to leave his den. However, when I came back half an hour later and turned on my flashlight, the skunk was in compartment No. 2, greedily eating a piece of comb containing brood. He did not seem to like this intrusion, for he immediately stopped eating and returned to his lair. Under these circumstances, it seemed best to discontinue my observations for that night. When compartment No. 2 was examined on the following morning, a few shreds of cotton were all that remained of the *fervidus* colony and nest.

I now became interested to know whether a skunk can also overcome large bumblebee colonies. On August 28, a nest of *B. impatiens*, containing at least 200 workers and numerous queens and males, was therefore placed in compartment No. 2, shortly after sunset. To my astonishment, this colony, too, was found completely destroyed on the following morning. This remarkable feat aroused my curiosity still more, and I decided to make a second attempt to see whether I could not find out how the skunk accomplishes such a hazardous task, for, as pointed out in Chapter VII, half a dozen stings of certain bumblebee species are sufficient to confine one to one's bed for a day or two.

In order to prevent the animal from returning to his den

after entering compartment No. 2, the sliding door between the two compartments was attached to a pulley so that the opening by which the two compartments were joined could be shut without much noise. After making this change, a colony of *B. impatiens*, consisting of about seventy-five workers, a few queens and males, and some brood, was placed in compartment No. 2 on August 30, soon after dark. At about 8 P.M., the skunk entered compartment No. 2, whereupon the door between the two compartments was closed. When I turned on one of my flashlights, the animal again tried to slink back into his den, and, finding the door closed, worked for over an hour at it, endeavoring to get back into compartment No. 1. But, about 9 : 15 P.M., he suddenly directed his attention to the bumblebee colony, and now the following, at times exceedingly comical, "melodrama"—the "music" was supplied by the bees—was enacted about two feet from my flashlights.

The first thing the skunk did was to scratch at the nest. This was immediately answered by a shrill chorus from within. As the workers came rushing out, they were seized one by one with the front paws, rolled on the ground for a few seconds with a quick, alternating, back-and-forward movement of both paws, and then eaten with a crunching noise. Occasionally the skunk would take a piece of cotton with which the bees had covered their comb, roll it in the manner described, and then examine it to see whether it contained any bees. From time to time he would make a frantic jump as a result of being stung by some worker which had eluded him. Such bees were usually grasped with the teeth and eaten without being rolled. Now and then the skunk tried to get at the comb, but in this he did not succeed until he had devoured

about half of the bees, when he quickly seized some of the brood, and, after carrying it into a corner, began to munch it with much relish. While thus engaged, he was several times painfully interrupted by prowling workers. After he had consumed this chunk of brood, he returned to the nest, and, having dispatched several more bees, took out another piece of comb and ate it. By 10 P.M. all the adults, as well as the comb, had been disposed of in this way, with the exception of one or two workers and several males which had made their escape by crawling through the wire cover of the compartment. Once or twice I saw the skunk eat a male without rolling it, but he invariably rolled the queens. When one of the latter accidentally fell into his drinking water, he scooped her out of the dish with one of his front paws, and then treated her in the same manner as he did the others.

On the evening of September 1, this experiment was repeated with a somewhat larger colony of *B. impatiens* before several students and a member of the faculty of the Bussey Institution. Although the skunk failed to work as well as he did two nights before, he had disposed of about a fourth of the colony and brood by 10 P.M., and by the next morning nothing remained of this colony and nest except some cotton, a few empty cocoons, and six or seven numb workers. On this occasion, the skunk was stung more frequently than during the preceding experiment, but apparently without any ill after-effects, for on the following day he readily ate beetles, crickets, grasshoppers, moths, and even full-grown woolly-bear caterpillars. Of these insects, the woolly-bears were rolled in the same fashion as the bumblebees, but more leisurely and for a longer period. The beetles, crickets, grasshoppers, and moths, on the other hand, he consumed without rolling.

The fate of the colonies referred to above no doubt frequently befalls bumblebee colonies out in the open, for I have found a considerable number of despoiled wasp and bumblebee nests, all bearing distinct indications of having been demolished by a skunk.

In addition to the enemies we have just been considering, there is man, who, intentionally or unintentionally, destroys many bumblebee colonies each year. Besides those which are plundered for the sake of the honey, a large number of surface nests are, no doubt, ruined by the mowing-machine or the hay-rake. It is fortunate for our bumblebees that the United States contains large areas which are mountainous or uncultivated where they may nest in comparative safety.

CHAPTER VII

PROTECTION AND DEFENSE OF NEST AND BROOD

Like all cold-blooded animals, honeybees and bumblebees have no means of regulating their body temperature, and thus exposure to cold invariably results in lethargy, and often death. On a sunny day in early spring I have often seen honeybees alight for a moment in front of the hive, where the ground was still frozen and partly covered with ice. Almost immediately they became numb and unable to fly, and though but a few inches from the hive, were unable to reach the entrance. When placed in a sunny spot they soon revived, and after circling about several times, entered the hive to deposit their load of nectar or pollen. In a honeybee colony, which normally comprises many thousands of workers, the bees crowd closely together on the comb when the temperature falls below 57° Fahrenheit, and in this way keep themselves and their brood from becoming chilled; nevertheless, during an exceptionally cold spell in early spring the bees are sometimes unable to cover all their brood, so that the larvae and pupae outside the cluster become chilled and die.

In the case of bumblebee colonies, the most populous of which—at least in the Temperate Zone—never consist of more than a few hundred individuals even at the time of their greatest prosperity, the matter of providing warmth for the brood is more difficult. Indeed, the first batch of larvae is entirely dependent upon the queen for food, protection, and warmth. However, it should be pointed out

that extremes of heat, as well as of cold, are harmful to bumblebees and their brood, which thrive best at a temperature of between 70° and 80° . If the temperature of a room in which bumblebee queens are confined drops much below 65° , they soon become numb, while if it mounts to 85° or 90° , they become restless and ill at ease.

Bumblebees, as was stated in Chapter I, almost always make use of deserted rodents' nests, on or below the surface of the ground. Usually a roof of wax is constructed over the comb as an additional protection against cold and dampness. Besides making it easy for the colony to maintain a more or less uniform temperature, an underground nest has the further advantage of being difficult of access for such enemies as *Brachycoma* and *Melittobia*; in fact, such species as *B. affinis*, *B. terricola*, and *B. impatiens*, which usually establish themselves at a considerable distance below the surface, very seldom fall prey to parasites, while species such as *B. fervidus* and *B. bimaculatus*, which often nest on or near the surface, are frequently victimized, especially by *Brachycoma*.

The larvae of bumblebees, unlike those of honeybees and wasps, are enclosed in a waxen envelope during their entire development, but even this covering, and the silken cocoons which they later spin about themselves, apparently do not always keep them sufficiently warm. However, as already mentioned, bumblebees overcome this difficulty, at least in part, by closely and, as it seems, affectionately embracing the cells containing their young, and incubating them (cf. Pl. I2).

Several attempts have been made to explain this singular habit, but there is still some difference of opinion as to its object, and the stimulus which causes the bees to act in such a manner. Hoffer (1882) has the following to say



PLATE VII.

Crab spider (*Misumena vatia*) with a worker of *Bombus affinis* var. *novae-angliae* in its fangs. About natural size.

concerning this activity: "While incubating, the queen frequently lies on the egg-cell in such a way that she warms it with her abdomen, as a hen does her eggs, the abdomen being closely pressed against the cell. Moreover, she also resorts to brooding in the case of older clumps of eggs and larvae, and the cocoons." A similar view is held by Sladen (1912), but this explanation is rejected by von Buttel-Reepen (1903), who suggests that, on the contrary, bumblebees, being guided solely by pleasant stimuli in such cases, probably incubate their brood because they enjoy the warmth which is given off by the larvae. Several well-founded objections to von Buttel-Reepen's theory have been published by Wagner (1907). Among other things, Wagner has pointed out that bumblebees incubate objects from which they cannot possibly get warmth, an observation which I am able to corroborate. Thus, for example, I have frequently seen queens and workers of various species incubate the outer rim of tin cans, even when the thermometer was below the optimum temperature for bumblebees. While external stimuli may be responsible for this habit to some extent, broodiness undoubtedly also depends upon a certain physiological condition. Only in this way, it seems to me, can one explain the fact that it sometimes takes several weeks for a confined *Bombus* queen to become broody, and that, after becoming so, she readily incubates various objects, such as tin cans, or the floor and sides of her nest-box, in some cases for days or even weeks before she lays her first eggs.

Whenever the air in the nest becomes too warm or damp, bumblebees resort to an interesting method of ventilation, somewhat similar in principle to our electric fan. This activity has given rise to a most fantastic story which will be described in more detail in the next chapter.

Bumblebees lavish a care on their young that almost borders on human affection, but the brood is not the only treasure the nest contains. Stores of honey and pollen attract not only insects, but also various other animals. With these valuable possessions to defend, bumblebees have need to be well armed, and they do not hesitate to use their sting with telling effect if occasion arises. They can make use of it repeatedly, and hence are more fortunate than honeybees, which lose their sting, and incidentally their life, when they employ this weapon. A bumblebee sting is very painful, and apparently more venomous than those of either honeybees or wasps. I have been stung several times by more than a dozen of these with no more serious after-effects than severe pain and swelling, while I have twice been obliged to take to my bed as a result of four or five stings from *B. fervidus*. The first time, I attributed my indisposition to ivy poisoning, but a repetition of the experience later in the summer left me no longer in doubt.

It is asserted by Wagner that one or a small number of bumblebees never attack an intruder, and that the courage of a bumblebee depends upon the number of individuals present. This certainly is not true of species like *B. americanorum*, *B. fervidus*, and *B. impatiens*. On more than one occasion I have been attacked by single workers of these species at the old nest-site while the remaining members of the colony were far away. As can easily be demonstrated, the temper of a bumblebee colony depends upon a number of factors. If, for instance, the colony is chilled, even savage species like *B. fervidus* exhibit little or no fighting spirit. This lack of temper becomes still more marked if, in addition, the colony has been compelled to fast. The ferocity of a bumblebee colony is also

modified to some extent by previous experience. If the nest of a savage species like *B. fervidus* is frequently disturbed, certain members of the colony will attack anyone whom they find in the vicinity of their nest. During the summer of 1925, I witnessed a most amusing scene in connection with a colony of this species which was kept in a large yard where a number of half-grown chickens were confined. Attracted by a frantic cackling, I hurried to the place and found several young roosters running about wildly, pursued by a vindictive worker of *B. fervidus*. I have also seen a team of horses take to its heels when attacked by several workers of this species.

In sharp contrast to the pugnacity of bumblebees when their nest is disturbed, is their peaceful demeanor while collecting nectar and pollen. One sometimes meets with the assertion that the workers of *B. americanorum* attack anyone who ventures near them while they are working on flowers. Although I have repeatedly disturbed queens and workers of this species while they were foraging, these individuals made no attempt to sting, and merely tried to escape when molested. It is quite probable, however, that foraging workers would show hostility if their nest were situated near the flowers from which they are gathering nectar and pollen.

In addition to their sting, bumblebees also make use of their legs and mandibles in defending their nest. When a bumblebee queen or worker is suddenly touched, she almost invariably raises one of her middle legs in a threatening manner, and if the annoyance continues, she usually lifts a second leg on the same side of the body, and may finally turn completely over on her back. In this position she may remain for a minute or more, with her mandibles wide open and the tip of her abdomen curved upward.

Sometimes one even sees her sting appearing with a droplet of venom near its tip. If a straw or a toothpick is presented to her, she often snaps at it angrily with her mandibles and occasionally clings to it so tenaciously that she may be lifted from the nest. Not infrequently, however, instead of grasping the object offered her, she expels a thin stream of liquid from her anus. This liquid is squirted for a distance of five to fifteen inches. On several occasions, I have seen two queens employ this interesting method of warfare against one another when they were placed in the same nest-box in spring. Huber (1802), who first described this behavior, supposed that the liquid ejected was the droplet of venom on the sting, and he further states that it does no harm, unless preceded by a perforation.

In order to determine whether Huber's assertion is correct, I pricked my finger with a pin and rubbed the liquid which had been ejected by an irritated worker of *B. terricola* into the wound, but found that it did not cause any pain. It is evident, therefore, that the liquid is not venom. The following observations may possibly also have a bearing on this question. I have frequently noticed that bumblebee queens, after having collected nectar from rhododendron, expel a watery liquid shortly after rising into the air. This is also true of honeybees, when they are fed with a thin sugar solution out in the open. Moreover, the quantity of venom produced is infinitesimal compared with the amount of liquid squirted.

As has already been pointed out, bumblebees, especially the more vicious species, are quick to attack with sting and mandibles if any vertebrate disturbs their nest. Similar punishment is meted out by many species if the nest is invaded by bees, such as *Psithyrus*, which do not

belong to the colony. However, as we shall see presently, one of our most common New England bumblebees, *B. fervidus*, acts very differently under these conditions.

On July 24, 1921, I noticed a disheveled *Ps. laboriosus* female crawling out from the nest-material of a colony of *B. fervidus*. She was wet all over, her pile being matted against the integument by a sticky liquid. On the same day a worker of a colony of *B. impatiens* which had been placed near the *fervidus* colony the preceding evening, was found sitting near the entrance to her nest, and, like the *Psithyrus* female, she too was completely covered with a sticky liquid. Whenever this worker attempted to enter her nest, she was immediately attacked and driven back by the other members of the colony. The reason for this strange behavior and the source of the sticky liquid, which I was at first unable to account for, were disclosed a few days later.

On July 27, I introduced a *Ps. laboriosus* female into a nest of *B. fervidus*, and was surprised to find that the workers, instead of creating a furore and killing the *Psithyrus*, as do the workers of *B. impatiens*, remained calm and resorted to a more peaceful, but equally effective, method of expelling the intruder. About a dozen workers gathered around the *Psithyrus*, and, after stealthily approaching a little nearer, each one placed a small droplet of liquid on the intruder with her mouth. The *Psithyrus* did not seem to relish this performance, and slowly left the comb, apparently seeking to hide herself. A number of workers followed her, and from time to time added more liquid, until she was as wet as the *Psithyrus* female and *Bombus* worker referred to above. The experiment was repeated with other *fervidus* colonies, and was later demonstrated before the Cambridge Entomological Club. The

members of the club were also shown the very different behavior of a colony of *B. impatiens* under similar conditions.

From July 27 to September 24, a considerable number of experiments were carried out in order to determine how colonies of *B. fervidus* react to other intruders. These experiments may be summed up briefly as follows: At various times, a young female of *Ps. ashtoni* and workers of *B. affinis*, *B. bimaculatus*, and *B. impatiens* were placed in the *fervidus* nest. All were daubed with liquid by the *fervidus* workers in the manner described above, but when a worker from another *fervidus* colony was introduced, it was attacked with legs and mandibles, and no attempt was made to daub it. During these experiments, the following animals were also placed in the nest-box: (1) worker honeybee, (2) male of *B. impatiens*, (3) male of *Polistes pallipes*, (4) bluebottle fly, (5) drone fly, (6) dragon fly, (7) small cricket, (8) gypsy moth, (9) young frog, and (10) a mouse. All of these were stung to death with no attempt at daubing. A katydid, however, was first daubed and then stung to death.

From these experiments it will be seen that the workers of a *fervidus* colony, at least when dealing with insects, vary their method of attack with the nature of the intruder. If the intruder is stingless, or if, like the honeybee, comparatively weak, it is seized immediately and stung to death, while daubing is invariably resorted to if the intruder possesses superior fighting ability. What enables the workers of *B. fervidus* to make these distinctions is difficult to say. In this connection it is interesting to note that bumblebees never molest certain intruders, such as the larvae of *Brachycoma*, even though the latter are very deadly to their brood.

At first there was some doubt as to the nature of the liquid which *B. fervidus* uses so effectively as a weapon, but I have finally come to the conclusion that it is honey, because (1) the liquid has a sweet taste; (2) a young *Ps. ashtoni* female that was being daubed, lapped up a drop of liquid which had accidentally adhered to some cotton; and (3) the *fervidus* workers themselves lapped up the liquid from the wings of a katydid after the latter had been stung to death.

During the summers 1921 to 1933, I had under observation a large number of colonies belonging to ten different species, but I never saw any colonies other than those of *B. fervidus* expel intruders by daubing them. It would be interesting to ascertain whether this method of defense is used by any other species. *B. fervidus* belongs to the Pocket-makers (*Marsipopoea*), and hence it is among the representatives of this group that we should first look for species which resort to daubing.

As already stated in Chapter IV, *Bombus* colonies are often infested by parasitic bumblebees of the genus *Psithyrus*. I have found *Ps. ashtoni* or *Ps. laboriosus* in one or more nests of all the common New England species, but not a single *Psithyrus* in the forty-six nests of *B. fervidus* which I have taken. It seems probable, therefore, that the daubing habit of this species plays an important rôle in preventing *Psithyrus* from breeding in its nests.

CHAPTER VIII

THE BUMBLEBEE "TRUMPETER"

About two hundred and fifty years ago, the Dutch painter Goedart (1700) published a comprehensive treatise on insects, Volume II of which contains a unique and probably the oldest account of the life-history and habits of bumblebees. This account seems to be based almost entirely on the author's own observations, and is of interest chiefly because of its many naïve anthropomorphisms. For example, Goedart states that the members of a bumblebee colony, besides keeping a "king" as do the honeybees, also have another individual among them which mounts to the top of the nest each morning about 7 A.M. and, like the bugler in the army, calls "his" companions to work by rapidly vibrating "his" wings, thereby producing a noise not unlike that of a drum. This performance, according to Goedart, lasts for about a quarter of an hour each morning, and was observed repeatedly by himself and others.

No one seems to have questioned this fantastic story until 1742, when the great French engineer and entomologist Réaumur published his observations on bumblebees. Although this famous scientist had a large number of bumblebee colonies under observation, he was unable to discover any behavior such as that described by Goedart, and therefore came to the conclusion that the "trumpeter" story was a fable. Réaumur's opinion in this matter naturally carried much weight, for it was accepted by such eminent entomologists as Kirby and Spence (1818). He

had dealt the bumblebee "trumpeter" a blow that was effective for almost one hundred and fifty years, when Goedart's story was again revived by the well-known Austrian bumblebee student Hoffer (1882).

Being acquainted with the contradictory assertions of Goedart and Réaumur, Hoffer tried for a number of years to find a "trumpeter" among the numerous bumblebee colonies which he had under observation, but his efforts were unsuccessful until the summer of 1881. On July 7 of that year, Hoffer obtained a strong colony of *B. ruderatus*, and placed it in a window facing southeast. Early the following morning his attention was suddenly attracted by a peculiar humming in the nest-box, and, upon investigating, he noticed that the sound was produced by one of the larger bees which was perched on top of the waxen envelope, and was vigorously vibrating her wings. Overjoyed at having rediscovered the long-sought "trumpeter," he aroused his wife and children, and later also called in the neighbors to witness the performance. Hoffer's "trumpeter" or "trumpeterette," as she ought to be called, was evidently somewhat of a slave-driver and rather persistent as compared with Goedart's, for "with painful regularity" she called her companions to work every morning shortly after three o'clock, and continued her "trumpeting" for about an hour. Hoffer now became interested to know what would happen if he removed the "trumpeter" from the colony, and, on doing so, found that thereafter the "trumpeting" was attended to by another member, although about an hour later than before. As the colony grew smaller toward the end of the summer, the activities of the "trumpeter" became more and more irregular. This, and the fact that one of his former students reported that he had heard a "trump-

eter" in a colony of *B. lapidarius*, led Hoffer to the conclusion that only *B. ruderatus* and perhaps some other underground nesting species have "trumpeters," but only while the colony is large.

Hoffer's confirmation again brought the "trumpeter" story into good repute among biologists for a period of more than twenty years. With the exception of Pérez (1889), it was accepted by numerous bumblebee students, in most cases after personal verification. Pérez, while not doubting the correctness of Hoffer's observations, rejected his interpretation, and pointed out (1) that there is little sense in having a "trumpeter" unless he be the first one to arise, and (2) that the sound produced by the "trumpeter" is of no use whatsoever, so far as arousing the colony is concerned, since, according to Pérez, bumblebees, like honeybees and ants, are completely deaf. He then offers a new explanation of this activity. After expressing the opinion that the bumblebee "trumpeter" fulfills no social function, and that the "trumpeting" is probably done for his own benefit, he suggests that the "trumpeters" in bumblebee colonies, like the so-called ventilators among the honeybees, are newly emerged workers which are exercising their wing muscles for the long flights that they will soon make.

The correct interpretation of this behavior was first suggested by an American farmer, Mr. J. Angus, in 1868. In a letter to Messrs. A. S. Packard and F. W. Putnam (cf. Packard, 1868), he writes as follows: "I have found the males [of *B. vagans*] plentiful near our garden fence, with a hole such as would be made by a mouse. They seem to be quite numerous. I was attracted to it by the noise they were making in fanning at the opening. I counted at one time as many as seven thus employed, and the sound

could be heard several yards off. Several males were at rest, but mostly on the wing, when they would make a dash among the fanners, and all would scatter and sport around. The workers seem to be of a uniform size, and fully as large as the males. I think the object of the fanning was to introduce air into the nest, as is done by the Honey-bees."

Thirty-five years later, the well-known German bee student, von Buttel-Reepen (1903), doubtless unaware of Mr. Angus's explanation, likewise suggested that the function of the bumblebee "trumpeter," like that of the ventilators in the honeybee colony, is to reduce the temperature, or to expel moisture or bad odors from the nest. Similar conclusions were reached by the Norwegian biologist, Lie-Pettersen (1906). This interpretation was accepted—in some cases after extensive experiments—by Wagner (1907), Lindhard (1912), Sladen (1912), and others.

More recently, however, Goedart's "trumpeter" story has found another adherent in Bachmann (1915). What is more, Bachmann has discovered that the bumblebee "trumpeter," besides arousing the members of the colony in the morning, also attends to the "curfew" in the evening. This performance he describes as follows: "At 8 : 30 the bumblebee trumpeter began his evening song. It was a rather long note, interrupted by a trill, as if a bumblebee were flying in the nest-box. But the trumpeter, standing on the comb, was only vibrating his wings."

The activity of the matutinal bumblebee "trumpeter" is vividly portrayed thus in German by Bachmann: "Exactly at 6 o'clock, a buzzing which lasted without interruption for two minutes arose in the nest. This immediately called to my mind the bumblebee trumpeter

which Hoffer discovered in a nest of *B. ruderatus*. My musician repeated his call three times, until the colony became active, and a bumblebee appeared ready for departure. At 6 : 26 a bustling worker dragged out a large larva, while the trumpeter exercised his art incessantly. Humming at first in the same pitch, the modulations became higher and deeper the longer they continued vibrating, then intermittently, like the noise of the Wagnerian hammer, or the discharge of electric sparks, finally like the slow roll of a drum, till the note became somewhat higher and then slowly died away.

"Now and then I clearly heard the beat of wings and thought that a bumblebee was flying close to my head. This reveille lasted from 6 : 44 to 7 : 06, hence for twenty-two minutes without interruption, and without the slightest disturbance on my part. Until 7 : 30 I three times heard a shorter call. Immediately thereafter, three bumblebees came crawling out of the flight-hole at the same time, after some had entered, laden with pollen, and the activities of Bumblebeetown came into full swing."

These two passages would not have been written, had Bachmann paid more attention to the literature of the preceding decade. As we have already seen, his assertions were disproved years before by the experiments of several authors.

During the past thirteen years, I have frequently had the opportunity to witness the behavior which gave rise to the "trumpeter" story. That the fanning of the so-called trumpeters has to do with the ventilation of the nest, and not with arousing the colony, or exercising the wing muscles, can easily be demonstrated by exposing a bumblebee colony to the rays of the sun. Of the thirteen colonies which I had under observation during the summer

of 1921, eleven were kept in windows facing south, and the remaining two in a window with a northern exposure. On every warm day, especially if the weather was sultry, one or more workers in each of the colonies on the south side of the building mounted to the top of the nest and began to fan shortly after the rays of the sun reached the nest-boxes. In a large colony of *B. impatiens*, the number of fanning workers sometimes amounted to more than a dozen. As soon as the sun receded from their nest-box, these "trumpeters" discontinued their work one after another, and crawled back into the nest. While this restless activity was in progress on the south side of the building, not a single bee, as a rule, was engaged in "trumpeting" in the two colonies on the north side, although one of these—also belonging to *B. impatiens*—consisted of more than 450 workers.

While "trumpeting" in a bumblebee colony is most pronounced when the nest is exposed to the rays of the sun on a hot day, it may also take place in the morning and evening—indeed, at any time. Thus, for example, I have occasionally found one or two workers fanning at various hours during the night, even when the temperature outside was less than 70° Fahrenheit. In this case, fanning undoubtedly has to do with the expulsion of moisture or disagreeable odors from the nest.

In order to determine whether "trumpeting" is resorted to only in large colonies, I placed the nest-box of a small colony of *B. impatiens*, consisting of a queen and two workers, in the sunlight. Three minutes later, one of the workers crawled to the top of the nest and began to fan, and within another minute the remaining worker and the queen appeared and assisted in this operation. To ascertain whether the "trumpeting" is done by newly

emerged individuals, as suggested by Pérez, I exposed the nest-box of a queenless colony of *B. fervidus*, containing no young workers, to the rays of the sun at 1 : 30 P.M., on August 14, 1922. At 1 : 34 a worker appeared on top of the nest, and, after crawling about a few seconds, began to fan vigorously. By 1 : 36 two more workers were engaged in this activity, and by 1 : 38 the number of "trumpeters" had increased to six. As *B. fervidus* frequently nests on the surface of the ground, this experiment incidentally confirms the observations of Wagner, who, contrary to the belief of Hoffer and Sladen, found that "trumpeting" is resorted to by surface-nesting species, as well as by those which have subterranean nests.

If a bumblebee nest is situated on, or near, the surface of the ground, its location is sometimes betrayed by the "trumpeting" of the ventilators. On several occasions, when I was about to take a colony shortly before sunrise, this low humming could be distinctly heard issuing from the tunnel at a distance of five to ten feet from the nest.

CHAPTER IX

HIBERNATION

Although our knowledge concerning the life-history and habits of the various species of bumblebees which occur in arctic regions and in the Tropics is rather meager, it seems to be definitely established that the colonies of at least some of the tropical species are perennial, while those of arctic species perhaps last only a month or two. In fact it has been suggested by Sparre-Schneider (1909) that some of the arctic species, such as *B. hyperboreus* and *B. kirbyellus*, are solitary in certain parts of the Far North. This hypothesis, though interesting, still lacks confirmation.

In the Temperate Zone we have conditions which are more or less intermediate between these two extremes. In the milder parts of the Temperate Zone, such as Corsica, Sardinia, and New Zealand, bumblebees may be seen on the wing throughout the year, but their colonies, although persisting during the greater part of the year, are probably not perennial. Similar conditions, no doubt, obtain in certain parts of the United States, such as the warmer regions of the South and the southern sheltered rim of the Pacific Coast. However, in the colder parts of the Temperate Zone, such as New England and Central Europe, we have a climate which more closely approximates that of the arctic regions, the only difference being a somewhat longer period of activity during the summer. Here in the vicinity of Boston, this period of activity usually lasts from three to six months (about April 15 to October 15),

depending upon the weather and the species. During the remaining six to nine months the young queens—the only caste which survives our rigorous winters—go into hibernation.

According to Sladen (1912), the young queens of some of the European species hibernate in the ground, while others creep into moss, thatch, or heaps of rubbish. The observations of this author were made chiefly on *B. terrestris* and *B. lapidarius*. Concerning these he has the following to say: "Both species pass the winter in much the same situations, but *terrestris* likes best to burrow in ground under trees, while *lapidarius* prefers a more open position, almost invariably choosing the upper part of a bank or slope facing north or north-west, though generally near trees." He goes on to tell of finding great numbers of young *lapidarius* queens hibernating near each other in such banks, in burrows from one to three inches long, and assumes that they choose a bank facing north in order to avoid being awakened too early in spring, when, as he says, they are very susceptible to a rise in temperature.

This account agrees with Hoffer's (1882), but Hoffer states that the young queens prefer a slope facing east for their *hibernaculum*, and that they spend the winter below the frost-line, "deep in the bowels of the earth." As will be seen later, the assertions of both these authors will have to be considerably modified.

Late in the summer of 1922, some workmen showed me a hole in a level grass-covered spot, into which they had seen a number of bumblebees crawl, but I did not have an opportunity to ascertain whether this was the entrance to a bumblebee nest until October 15. Unfortunately I lost track of the tunnel as soon as I began to work, and although I dug down several feet, I was unable to

discover any nest. I was rewarded, however, by finding twenty-one queens of *B. impatiens* hibernating in the sod about the hole. All of them were numb, but after being exposed to the comparatively mild air for a few minutes, several took wing. Having read Sladen's account concerning the hibernation of *B. lapidarius*, I came to the conclusion that these twenty-one queens had chosen this particular spot in which to spend the winter, because they had found it especially suitable for the purpose, but the following observations—made since that time—have convinced me that there are other reasons than those suggested by Sladen why the young queens of certain species of *Bombus* are sometimes found hibernating near each other in large numbers.

On October 2, 1923, I made an unsuccessful attempt to dig up a colony of *B. impatiens* in a level and rather sandy spot in the Arnold Arboretum. During this operation I discovered thirteen young queens of *B. impatiens* hibernating a few inches below the surface of the ground, within a radius of about two feet. This led me to surmise that the young queens of *B. impatiens* usually hibernate near the maternal nest, and that the hole about which I had found the twenty-one hibernating queens on October 15, 1922, was probably the entrance to a bumblebee nest, as was asserted by the workmen who showed it to me. The following observations furnished additional proof for this assumption.

On October 6, 1923, I dug up a nest of *B. impatiens* in a sandy slope facing southwest. Near the entrance I found over thirty hibernating queens of this species, while the nest itself contained, in addition to the old queen and several workers and males, about a dozen more young queens which had not yet gone into hibernation.

In order to determine how the young queens of *B. impatiens* prepare their winter home, I decided to make further investigations. An excellent opportunity for this purpose was provided by an unusually large colony of *B. impatiens* which was discovered in the Arnold Arboretum on August 15, 1926. During the early part of September, young queens could be seen leaving and entering the tunnel whenever the weather was pleasant. On September 26, more than forty of them were busily at work digging their *hibernacula* in the sod surrounding the nest entrance. Scattered among the little mounds of soil which these young queens had piled up were many others which had been made earlier. Near each one of these was a cavity, about one-half of an inch in diameter. A few of the mounds were examined, and in almost every one a young queen of *B. impatiens* was found at a depth of about two or three inches. The place was again visited on October 1 and 17. By this time, most of the little piles of soil had been washed away by rain, and the openings to the *hibernacula* were closed, but on both of these visits a number of young queens were still digging themselves in. By November 11, the piles of soil had disappeared, and no openings could be seen. Several pieces of sod were turned over within a radius of about four feet of the nest entrance, and each contained from two to five queens of *B. impatiens*. These buzzed slowly but angrily and protruded their stings, near the tip of which could be seen a small droplet of venom. It was estimated that from 200 to 300 young queens of *B. impatiens* were hibernating at this place.

In this connection some observations of Huber (1802) and Hoffer are of interest. On August 21, the former took a nest of *B. muscorum* containing only a few young queens, but he discovered about thirty-five others in a small

cavity, connected with the nest by a narrow passage. From this he concluded that these queens would have hibernated in the cavity if they had not been molested. But since young queens habitually retreat to such cavities, if available, whenever their nest is disturbed during the summer and fall, Huber's assertion need not be taken too seriously, especially when one considers that this nest was examined rather early in the season. The same author also mentions a bumblebee nest in which no workers or males were found, although a single young queen was occupying a small cavity in the soil below the nesting-material. She was not yet numb, and flew away as soon as disturbed. From these two observations, Huber concludes that the young bumblebee queens dig their *hibernacula* in the soil near the maternal nest. Similarly, Hoffer dug up a once populous nest of *B. lapidarius* in the middle of October, 1881, but it contained only fragments of moldy comb and five dead workers. However, in some chewed-up grass in a depression about two feet from the nest, he found a lethargic queen of *B. lapidarius*, whose glossy pile indicated that she had been reared during the preceding summer. Hoffer also reports that he discovered hibernating *lapidarius* queens "without a trace of grass" in holes which they had dug themselves, presumably near this same nest, although his account is not entirely clear.

Being interested to know at what depth and in what state I would find the queens in the middle of winter, I pried loose a piece of sod, about nine inches square, near the nest entrance on February 5, 1927. On this day the minimum temperature was 10° Fahrenheit, and the ground was frozen to a depth of about six inches. The piece of sod was broken up with a pick, and during this operation three queens of *B. impatiens* were obtained. I

then dug down several feet, but found none in the soil below the frozen layer, where, according to Hoffer, they might be expected to occur. Of the three queens, No. 1 had been completely crushed by the pick, No. 2 had lost part of one hind leg, but No. 3 was uninjured. Although firmly imbedded, these queens had maintained a sufficiently high body temperature to prevent them from freezing solid. Probably as a result of the accident to her leg, queen No. 2 was feebly moving when first noticed, while No. 3 appeared to be dead. During the ten-minute walk home, I carried queens No. 2 and 3 in the hollow of my hand, and by the time I entered my room, queen No. 3 also began to show signs of life by slightly twitching her tarsi. After being exposed to a temperature of about 65° for a few minutes, both queens feebly vibrated their wings when disturbed, but did not show their stings. Half an hour later, they began to crawl about, and on February 8 they were exhibited before the members of the Cambridge Entomological Club. On the following day queen No. 3 was found dead.

Two more young queens of *B. impatiens* were dug up on March 26, within a few inches of the spot where the first three had been hibernating. Like No. 2, queen No. 4 had lost the tarsus of one of her hind legs, but No. 5 was uninjured. Although the ground was no longer frozen, these queens were still numb, but were able to vibrate their wings slowly, and, after being held in the hollow of my hand for a few minutes, they gradually lost their lethargy and began to crawl about. They were confined with No. 2, and exhibited certain peculiarities of behavior toward one another which will be described in a subsequent chapter.

On April 19, 1927, an exceptionally pleasant day, I noticed many queens of the earlier-appearing species,

including several of *B. impatiens*, collecting nectar on rhododendron. The hibernating place was therefore visited late in the afternoon with the hope of seeing some of the young queens emerge from their winter quarters. Although not so fortunate as to witness this, I was rewarded by discovering several emergence holes near the old nest entrance. I visited the hibernating place again at 10 A.M. the next day, when the thermometer registered between 70° and 80°, later reaching a maximum temperature of about 90°. On my arrival I found more than half a dozen queens of *B. impatiens* basking in the sunshine among the dry leaves within about five feet of the spot where the old nest entrance had been. From time to time, other queens scurried over the leaves and hid beneath them, as if to avoid the scorching rays of the sun. These queens, no doubt, had just emerged from their *hibernacula* in the cool soil. When thrown into the air, they flew but a short distance, and then quickly crawled under the leaves, where they seemed to fall into a sleep-like stupor. Approximately fifteen queens in all were seen at the hibernating place in the course of an hour. About 10 : 30 A.M. I heard a muffled buzzing in the earth at the base of an old stump on which I was sitting, and, upon investigating, found a young queen of *B. impatiens*, which I dug out and placed in the hollow of my hand. Her pile was rather wet, but it dried in a few minutes. After having expelled a considerable quantity of yellowish-green faeces, she cleaned herself and then remained quiescent for a long time, as if dozing, the tips of her antennae meeting in front of her mandibles as is sometimes the case with dead specimens.

From the foregoing observations, it is evident that the young queens of *B. impatiens*, and probably also those

of its close Old World relative, *B. lapidarius*, under normal conditions hibernate in the soil near the entrance to the maternal nest.

It would be interesting to ascertain where the bumblebee queen spends the night before she has succeeded in finding a nest-site. Réaumur (1742) states that one spring he noticed bumblebee queens digging holes in a slope in his garden, and Sladen, who saw about twenty *lapidarius* queens trying to burrow into a grassy bank in June, suggests that "they had been hibernating in the bank and were endeavouring to return to their burrows." Whether or not the queens of *B. impatiens* return to pass the night in the soil about the maternal nest after emerging from their *hibernacula* remains to be determined.

I have repeatedly dug in places where, according to Sladen, one should expect to meet with numbers of hibernating queens, but I have never succeeded in finding more than a single individual, and that only on two occasions. On July 7, 1925, while taking a colony of *B. terricola* in a sandy and densely wooded slope facing north, I accidentally came upon a young queen of *B. bimaculatus* imbedded in the cool sand, about six inches below the surface. Although quite drowsy at first, she soon became active and flew away. Similarly, on August 6 of the same year, a young *terricola* queen was discovered in a state of lethargy in the loose soil near the old nest-cavity of a colony of *B. impatiens*. Hence it seems probable that when Sladen found so many young queens of *B. lapidarius* in one spot, he was unwittingly dealing, as I did in 1922, with a former nest-site.

It must be pointed out, however, that hibernation in the soil about the maternal nest is not a fixed and unalterable instinct with the queens of *B. impatiens*. During

the past thirteen years I have transferred about fifty colonies of this species to nest-boxes. Some of them were placed in a third-story window of the Bussey Dormitory facing south, others in a second-story window facing north, and the rest on two boards in a partly covered, abandoned cellar. The boards were about two and six feet respectively from the cellar floor, the higher one on a level with the ground outside the cellar. The soil below the windows of the dormitory, as well as that around the cellar, was covered with sod similar to that in which I had found large numbers of hibernating queens of *B. impatiens*, while the floor of the cellar was barren and covered with a considerable quantity of sand. Although hundreds of young queens of *B. impatiens*, as well as those of other species, were reared in both of these places, none were found hibernating in the ground nearby.

Having established the fact that under favorable conditions the young queens of *B. impatiens* hibernate in the earth about the entrance to the maternal nest, I was curious to know whether the young queens of some of our other New England species have the same habit. To this end a large colony of *B. affinis*, discovered during the first week of September, 1925, was left undisturbed, since many young queens were observed entering and leaving the nest, the tunnel of which opened among some old leaves in a wooded part of the Arnold Arboretum. On November 21, 1925, I dug about the nest entrance, but all my efforts failed to disclose a single queen. Similar investigations were made during the fall of 1926 in connection with a large colony of *B. fervidus*, nesting in an open, grass-covered slope. On September 25 a number of young *fervidus* queens were seen entering and leaving the tunnel. But when the deserted nest was dug up on November 11,

not a queen was found hibernating in the sod about the entrance, although in both this and the preceding case, conditions seemed to be ideal for the purpose. While it is not advisable, as a rule, to base conclusions on negative evidence, the foregoing observations nevertheless make it probable that the young queens of *B. affinis* and *B. fervidus*, unlike those of *B. impatiens*, do not, under normal conditions, hibernate near the maternal nest.

According to Wagner (1907), the beginning of hibernation depends upon the weather, and he further states that bumblebee queens reared in well-protected nests below the surface of the ground, or in haystacks, take up their winter quarters later than those reared in surface nests. These assertions are true neither of the European nor of our American species. In Europe, the queens of *B. pratorum*, a species which frequently nests in the ground, begin to hibernate in July, while those of such surface-nesting species as *B. agrorum* and *B. muscorum* do not take up their winter quarters until at least a month later. Here in the vicinity of Boston, the nests of *B. bimaculatus* and *B. terricola* are almost invariably subterranean, and yet most queens of these two species go into hibernation in July, while those of *B. fervidus* and *B. vagans*—species which usually nest on or near the surface of the ground—do not begin to hibernate until the latter part of August. These facts show that the beginning of hibernation depends on the species, rather than on the weather, or the location of the nest.

Several attempts have been made to winter bumblebee queens in captivity. Sladen seems to have been the first to make experiments along this line. In the fall of 1910, and again in 1911, he confined some queens of *B. lapidarius*, but all his endeavors to have them hibernate were

futile. Better results were obtained by the Danish biologist, Lindhard (1912), who, although failing the first time, finally succeeded in wintering a number of young *terrestris* and *lapidarius* queens. Here in America, similar experiments have been successfully carried out by Frison (1927). The following attempts which I made to winter young queens of *B. impatiens* may also be of interest.

Of the twenty-one hibernating queens of *B. impatiens* dug up on October 15, 1922, sixteen were placed in a box containing about six inches of soil. The queens refused to dig themselves in, probably because the conditions were not suitable, and by December 26 all but four had died. When disturbed, these four queens, numb from cold, began to vibrate their wings very slowly, and although no longer molested, continued to do so for several minutes, as if unable to stop. None of these queens survived the winter.

On October 6 of the following year, about thirty young queens of *B. impatiens* which were found hibernating near the entrance of a nest taken on that day were confined in wire cages, from which the bottoms had been removed. These cages, three feet high, were then lowered about a foot into the ground to prevent the queens from escaping. By October 14, all had dug themselves in, but apparently only three survived the winter, the first one appearing on May 14, 1924, and the other two on May 15. Of the remaining queens there was no trace.

Hibernation is one of the phases in the life-history of bumblebees which has hitherto received little attention. As we learn more concerning this habit, it will no doubt be found that, as in many other respects, the various species and groups of bumblebees have their own peculiar methods of spending the winter.

CHAPTER X

REARING OF COLONIES IN ARTIFICIAL NESTS

The biologist who attempts to give a complete account of the life-history and habits of the bumblebees of any part of the world is generally confronted with the following difficulties: (1) he rarely, if ever, has the opportunity to observe the founding of a bumblebee colony and its early stages, and (2) it is usually impossible for him to study the habits of the less common species, because he is unable to procure their nests. The first attempts to overcome these difficulties were made by Hoffer (1882). This eminent bumblebee student confined a large number of *Bombus* queens in a museum at Graz, and thus was able to observe how the queen of *B. lapidarius* constructs her nest and the first egg-cell. However, none of these experiments produced a colony. Better results in rearing some of the European species under artificial conditions were obtained by Lindhard (1912) and Sladen (1912), while in this country, Frison (1918 and 1927a) has secured quite a number of colonies by confining queens of our North American species.

I became interested in this subject in 1921, and have since then successfully reared twenty-three colonies belonging to ten American species, among them a colony of *B. ternarius*, a species which is exceedingly rare in the vicinity of Boston. During the following six summers, a large number of queens belonging to eleven of the thirteen New England species listed by Franklin (1912) were captured for further experimenting. The queens were

confined in individual wooden nest-boxes, the majority of which measured about $9 \times 6 \times 4$ inches. Each nest-box was provided with a double cover, the lower one of glass and the upper of wood. At the anterior end of the box, a round opening, about half an inch in diameter, which could be closed by means of a cork, served as a flight-hole. A small piece of honeybee-comb foundation, partly surrounded with a layer of cotton as nesting-material, was then firmly pressed to the bottom of the nest-box near the opposite end. A tin can, about three inches in diameter and two inches high, from which the cover had been removed, was turned upside down over the foundation and cotton, after a hole had been made in the rim, through which the queen could readily pass. Every two or three days, a fresh supply of honeybee pollen was provided for her on the layer of wax within the cotton ring, and each morning a shallow porcelain dish, which I kept outside the tin can, was thoroughly cleaned and replenished with liquid food, consisting of about two-thirds water and one-third honey. In order to keep the nest-box as sanitary as possible, a small quantity of dry sand was scattered in one of the corners of the box, near the flight-hole.

When a queen is confined, it usually takes considerable time for her to become broody, but after she has once oviposited, the tin can may be removed and more nesting-material added to enable her to keep the brood sufficiently warm. The nest-box may then be placed in a shady, protected spot, and the flight-hole opened, so that the queen can forage for herself. This rather simple method of starting a colony was employed, because queens which have laid their eggs in confinement, and are later discarded, usually return to the place from which they have been released. Thus, during the summer of 1925, I kept

several queens of our more common species in nest-boxes, and as soon as each had oviposited, I gave her complete liberty. Although some of the queens failed to come back, a few colonies of *B. vagans* and *B. impatiens* were reared in this way. If the queen belongs to a rare species, and one does not wish to run the risk of losing her, it is best to keep her confined until the first workers emerge. Even then there is danger of her not returning, should she feel inclined to take a flight, but this can be prevented by narrowing the flight-hole so that only the workers can pass through.

As has been stated, it generally requires some time for a queen to become broody, but if two queens of the same species are placed together, they usually settle down much more quickly. Almost invariably, however, one kills the other when the first eggs are laid, and the remaining queen is sometimes rendered useless for further breeding experiments because of injury to one of her antennae or legs. An interesting exception to this rule is the behavior of two queens of *B. impatiens* which were dug out of their *hibernacula* on March 26, 1927, and confined in the same nest-box. No. 1 had lost the tarsus of her right hind leg when she was taken from her winter quarters, but No. 2 was unharmed. Within a fortnight they had each constructed a honey-pot, but there was only one clump of brood, which apparently belonged to both, since the two queens were frequently seen incubating it side by side. They tended the larvae assiduously, and after the latter had developed into pupae, they could often be seen lying at the base of the cocoons, head to head, with their abdomens meeting behind, or the head of one touching the tail of the other. On sunny days the nest-box was placed out of doors and the flight-hole opened, so that the queens

could forage. Queen No. 2 was frequently seen to take advantage of this opportunity, but queen No. 1 apparently never left the nest. On May 17 it was noticed that queen No. 2 had lost one of her antennae, and six days later she was found dead in the nest-box. Whether she had been stung to death by queen No. 1 could not be determined. Although these two queens were without question reared in the same nest, I doubt that this was the reason for their harmonious relations with each other.

Another method of rearing bumblebee colonies, which can be employed later in the season, is to confine two or three workers with a queen of the same species. In this way I have succeeded in establishing a number of colonies of our more common North American bumblebees. As a rule, this method of starting a colony is not feasible in the case of rare species, since it is difficult or impossible to obtain workers, but as will be seen from the following experiments, workers of another species may sometimes be substituted.

On June 6, 1922, a queen of *B. ternarius* was captured in the Arnold Arboretum and confined in a nest-box. As she took no interest in the nesting-material, three workers of *B. bimaculatus* were placed in her box on June 14, but she would have nothing to do with them, and, three days later, the *bimaculatus* workers were replaced by two small workers of *B. impatiens*. With these two workers the *ternarius* queen made friends, and shortly afterwards began nest-building. The first batch of eggs was laid about June 21, and the first *ternarius* worker hatched on July 14. By July 16, six more workers had emerged. The two workers of *B. impatiens* were then removed, and the young *ternarius* colony was left to shift for itself. By August 13, the number of workers had increased to seventeen, and

within a few weeks, several newly hatched *ternarius* males were present in the nest. At the beginning of September, the queen showed signs of becoming feeble, and on September 10 she disappeared. The last workers died during the first week of October.

However, all my efforts to rear colonies in this way of some of the other rare species, such as *B. borealis* and *B. americanorum*, proved futile, since it was impossible to find workers which would coöperate with the queens of these two species. Thus on May 29, 1922, I confined a queen of *B. borealis* with two workers of *B. fervidus*, and on June 6 a second *borealis* queen with three workers of *B. impatiens*, but on June 25 the first one was found dead in the nest, whereupon all the workers were liberated, neither queen having started a colony. Similarly, on May 29, 1922, I placed a queen of *B. americanorum* and three workers of *B. fervidus* in a nest-box, but she remained restless and refused to associate with them. Another *americanorum* queen was therefore substituted on June 5. Although hostile to the *fervidus* workers, queen No. 2 constructed an egg-cell and oviposited on June 11, but the larvae were not fed and died shortly after hatching. Both *B. fervidus* and *B. americanorum* are Pocket-makers; that is, they feed their larvae, at least those destined to be workers, through one or more pockets (cf. Pl. X2) which they construct at the side of each group of larvae. On returning from the field, the foraging bee deposits her load of pollen directly in these pockets, through which it later reaches the larvae. The Pocket-makers therefore probably let their worker larvae die, when they are unable to provide them with food in the usual manner. If this supposition is correct, it will be impossible to rear colonies of the Pocket-makers by con-

fining queens, unless the latter are permitted to collect pollen from flowers.

A simple way of inducing a *Bombus* queen to become broody and oviposit is to furnish her with a few cocoons containing living pupae, but this method, like the preceding one, can be employed only comparatively late in the season. Several queens may sometimes be supplied by dividing the brood of a nest which is already in an advanced stage. If a queen is given cocoons belonging to her own species, she is almost certain to adopt them at once, but since queens not infrequently adopt those of other species, I became interested to know whether I could make use of this habit to rear colonies of *B. borealis* and *B. americanorum*. The following experiments were therefore carried out.

On June 26, 1922, about a dozen cocoons of *B. impatiens*, from which workers were just beginning to emerge, were presented to the *borealis* queen which had previously been used in the experiment with three workers of *B. impatiens*. She immediately showed an affection for both the cocoons and the workers which hatched from them. On June 28 she constructed an egg-cell and oviposited, and two days later this mixed colony was permitted to forage out in the open. But when the nest was examined on the following day, the queen was missing and did not return.

On July 2 of the same year, another *borealis* queen was captured and confined with sixteen worker cocoons of *B. impatiens*, which were adopted at once, as in the preceding case. On the following day she, too, built an egg-cell and oviposited. By July 5, four workers of *B. impatiens* had emerged, whereupon the nest-box of this *borealis-impatiens* colony was placed out-of-doors and the

flight-hole opened so that the bees could forage for themselves; but eight days later the queen was found dead, probably as a result of an encounter with the workers.

On July 8 a fourth *borealis* queen was given fourteen worker cocoons of *B. fervidus*. She laid a batch of eggs on the following day, and another on July 11. Meanwhile several *fervidus* workers had emerged, and after July 13 the colony was allowed to forage in the open. For a time, the members of this *borealis-fervidus* colony seemed to live together peacefully, but on July 19 it was noticed that the *fervidus* workers kept the *borealis* queen from the comb by daubing her with honey, a habit which has been described in Chapter VII. In spite of this treatment, the queen lingered about the nest until August 18, when she died. During the first part of August, a number of *fervidus* males hatched, but no adults of *B. borealis* were reared.

Similar results were obtained in experiments with *B. americanorum*. On June 26, 1922, queen No. 2 was again confined, this time with about a dozen cocoons of *B. impatiens*, to which she immediately became greatly attached. She showed no hostility toward the workers that emerged, and two days later constructed an egg-cell and laid a batch of eggs. On July 2 this mixed colony was placed out of doors so that it could forage for itself. Everything went well until July 6, when the queen was found dead in the nest, having probably been killed by the workers.

On July 26 of the same year, a third *americanorum* queen was confined with an *americanorum* worker and sixteen cocoons of *B. fervidus*, and on August 2 another *americanorum* worker was added to this nucleus. The cocoons were readily adopted, as were the *fervidus* workers which hatched from them. On August 3 the queen built

an egg-cell and oviposited, and shortly afterwards this mixed colony was given its liberty. *Americanorum* worker No. 1 did not return, but No. 2 and some of the *fervidus* workers brought in one load of nectar and pollen after another. For several days the colony prospered, but on August 10 it was noticed that the *fervidus* workers were daubing the *americanorum* queen and worker with honey. On the next day the *americanorum* worker failed to return, but the queen, although her pile was constantly soaked with honey, lingered about the nest until August 21, when she disappeared. A few days later a number of *fervidus* males emerged, but no adults of *B. americanorum* were produced by either of these colonies.

Somewhat better results were obtained in the summer of 1923, when about fifty worker cocoons of *B. fervidus* were given to an *americanorum* queen. Although, as in the preceding case, the queen was daubed with honey by the *fervidus* workers, and thus kept away from the comb most of the time, several *americanorum* queens and workers hatched from the eggs which she laid while the *fervidus* workers were still in their cocoons, but most of the young produced by this mixed colony were males of *B. fervidus*.

By the various methods described in the foregoing paragraphs, I have succeeded in rearing more than twenty colonies belonging to ten species, as follows: *affinis*, 1; *terricola*, 1; *bimaculatus*, 2; *impatiens*, 9; *perplexus*, 1; *ternarius*, 1; *vagans*, 4; *separatus*, 2; *americanorum*, 1; and *fervidus*, 1.

It has been asserted by Wagner (1907) that a bumblebee which gets into a nest of another species is invariably treated as a member of the colony, after it has been in the nest from ten to twelve hours. That this statement, and incidentally his belief that the specific odor of a bumblebee

colony emanates only from the queen, is incorrect, is shown by the fact that members of such closely related species as *B. fervidus* and *B. americanorum* may refuse to have anything to do with each other, even after they have been together for weeks, and although the members of one species have been reared by the other.

CHAPTER XI

FINDING AND TRANSFERRING OF COLONIES

Nearly all the bumblebee colonies which I had under observation as a boy were discovered accidentally while roaming through the fields and meadows, but during the past few summers I have resorted to other, more dependable methods of locating colonies. Although I have repeatedly tried to find nests by "lining," a method usually employed in searching for bee-trees—that is, hollow trees in which escaped honeybee colonies have taken up their abode—I have never succeeded in locating a bumblebee colony in this manner. More satisfactory results were obtained by spending an hour or so on some grassy bank, or, better still, on plowed land which had been lying fallow for a year or more without being harrowed. In such places I have on several occasions found as many as six to a dozen nests in a single afternoon.

An excellent opportunity for locating bumblebee colonies presents itself each year during the haying season, for as soon as the grass near a bumblebee nest is cut, the workers returning from the field become disoriented, and by their frantic search often betray the nest-site. Not infrequently one finds quite a number of bumblebee nests within a comparatively small area.

A striking example of this is a sloping piece of ground, about one-fourth of an acre in size, which was plowed but not harrowed in the fall of 1923. During the three preceding summers this area did not harbor a single bumblebee colony, but after it was plowed, numerous field mice built

their nests in the crevices beneath the furrows, and since that time from ten to twenty bumblebee colonies have been found each year occupying some of these nests. In the summer of 1926, eight bumblebee colonies were taken on this piece of ground, within a triangular plot measuring about ten square yards.

Having finally discovered a bumblebee nest, we are confronted by a more strenuous and exciting task—the taking and transferring of the colony. As a boy, my procedure in dealing with a surface nest was briefly as follows: I provided myself with a large cigar-box, covered the bottom of it with a layer of dry sand, and at one end bored a flight-hole which could be closed by means of a cork. Thus equipped I went to the spot inhabited by the bumblebee colony, seized the nest with both hands, dropped it into the box, and quickly clamped down the cover. A hole sufficiently large was then dug at the former nest-site, and the box inserted in the cavity in such a way that it projected about an inch above the ground. The space around the box was then filled with earth and the cover removed, whereupon the normal activities of the colony were soon resumed. About sundown, when most of the foraging workers had returned from the field, the nest-box was closed and transferred to a shady, protected part of our garden. But the bees were not given their liberty until the next morning, in order to prevent the more venturesome from escaping through the flight-hole and becoming lost during the night.

But the taking of subterranean nests was usually not such a simple matter, especially in the case of such species as *B. lapidarius* and *B. terrestris*. Whenever a large colony of one of these two species was dug up, it was necessary to drive away all the workers issuing from the

tunnel, as well as those returning from the field. Not infrequently, however, some of the workers refused to be put to flight, and, as a result, I was often severely stung.

Since the summer of 1921 I have made use of an easier and more satisfactory method of taking colonies, which, except for a few minor modifications, is essentially that described by Sladen (1912) in his admirable work on the English species. The equipment which I generally carry in my knapsack for this purpose consists of the following articles: first, two wide-necked glass jars—preferably of the type in which mayonnaise dressing is sold—the metal covers of which have been stripped of all paper and perforated in as many places as possible so as to provide sufficient ventilation; secondly, two pieces of window glass, each about two inches wide and five inches long; and lastly, a large trowel. For small or medium-sized colonies I have found it most satisfactory to use a pint jar, and another of half-pint size. The smaller jar should be of such dimensions that it will not pass through the neck of the larger one. When dealing with more populous colonies it is best, as a rule, to use a pint and a quart jar. These few tools ordinarily suffice to take surface nests, as well as those underground having short tunnels, but when dealing with colonies of *B. affinis* and *B. impatiens*, whose nests are not infrequently situated at a considerable depth, a strong spade is indispensable. For longer trips it is therefore advisable to provide oneself with a good spade, and, if the country is wooded, with a hatchet for cutting some of the larger roots.

Although a bumblebee colony can be taken at any hour of the day, it is generally more satisfactory to do so just before sunrise, since the bees seem to be less pugnacious

at that time, not to mention the fact that it is much easier to work during the cool morning hours. As the process of taking a surface nest, or one with a short tunnel, is—except for the digging—almost identical with that employed in taking one having a long tunnel, I shall describe only the procedure in transferring a fair-sized colony of an underground-nesting species, such as *B. affinis*.

After we have definitely located the entrance to the nest, we put the larger jar on a level spot and replace the cover with one of the pieces of glass. The other piece of glass we keep near the half-pint jar so as to have it ready when we need it. We now insert a pliable shoot of a shrub or tree into the entrance in order not to lose track of the tunnel while digging. This will probably bring out some of the guards which must be quickly caught in the small jar. We then turn the latter upside down over the large one and withdraw the two glass covers, so that the bees tumble into the jar below, the cover of which we quickly replace in such a way as to leave a narrow space for air. Meanwhile several workers may have returned from the field, but they are almost certain to depart as soon as they notice us. However, they will come back shortly, and it is therefore best, especially when dealing with a more vicious species such as *B. fervidus*, to step aside for a few moments and capture them when they alight. We are now ready to begin digging. As we proceed, we shall every now and then be greeted by one or more angry workers which must be caught before they have a chance to leave the cavity. Should the tunnel branch as we continue to dig, a few blows with the spade on the surrounding soil will usually cause one or more furious workers to scurry out of one of the tunnels. If no workers appear, it is advisable to insert a shoot into the second

tunnel as well, so as not to lose its location while we dig along the first. We may follow this one for several feet without encountering any bees; in that event we can be fairly certain that it does not lead to the nest, and we therefore direct our attention to the other. If we are on the right track, more and more workers will issue from the tunnel as we proceed, a sign that we are no longer very far from the nest. Suddenly, as we pry loose a large piece of sod, a number of workers may come madly rushing out, buzzing in loud protestation. At the same time we hear a threatening but muffled chorus, in which we can clearly distinguish the shrill note of the queen, and we know that we are within a few inches of our goal. In order to avoid being stung, we quickly retreat a short distance and wait until the bees have calmed down. We now discard the spade and capture several workers which are apparently keeping guard to prevent any new attack on their home. Then we carefully widen the tunnel with the trowel, meanwhile catching any bees which may appear. When we reach the nest, we make an opening large enough so that it may be easily lifted out, and gently tap against its side to see whether it contains any more workers. Some of these, especially the smaller individuals from the earlier broods, may not venture farther than the outer rim of the nesting-material where they usually fall upon their backs, ready to sting anything that touches them. If the nest is dug up in late summer, it almost invariably harbors one or more young queens and perhaps a few males, or, still more interesting, young males and females of *Psithyrus ashtoni*, and possibly even their mother. In either case, the Psithyri, as well as the young queens and males, will make no attempt to defend the nest, but will try to escape by taking wing, or hiding beneath the comb and in the crevices of the nest-

cavity. After we have caught most of these fugitives, we carefully place the trowel under the nest and draw it toward us. This may cause the old queen to come running out, buzzing loudly and shaking her wings in great agitation. But as she probably is no longer able to fly, she is easily caught and deposited in the jar with the rest of the colony. We can now fearlessly place our hand under the nest and lift it out of the cavity. After it has been put in a shady spot, and the nesting-material removed from the comb, one or more males may hurriedly crawl out from among the cells in an effort to escape. Since they have no sting, we can safely seize them with our fingers, and, on holding them a few moments in the hollow of our hand, we notice that they give off a pleasant odor. If we remove the glass cover, we shall find that the jar containing the colony has been perfumed with a similar fragrance, for each bumblebee species has its own characteristic odor which is especially pronounced in the males.

Several young workers, easily recognized by their ashy-gray pile, may also be hiding in the crevices between the cells. If these show any signs of hostility, it is best to catch them and drop them into the jar. The comb can now be placed in a box which has been lined with a thick layer of cotton to prevent the cocoons from becoming injured, for the bees which emerge from bruised cocoons are almost always cripples. As this entire operation will probably have taken over an hour, it is practically certain that we have secured all the workers which were foraging in the field. If any of the young queens have made their escape, we may wait until they return, which will very likely be within ten or fifteen minutes. Meanwhile we fill the cavity and level the ground, putting the old nesting-material on the spot where we began to dig. After circling about sev-

eral times, one young queen after another will finally settle down on the nesting-material, where she can be easily taken prisoner. But it is useless to wait for the reappearance of any males which may have evaded capture, for I have never known them to return. After fastening the metal lid on the jar containing the bees, we collect our implements and depart. During our journey home it is advisable to carry the jar upright in the knapsack, which ought to be kept closed, for bees calm down much more readily in the dark.

Upon our arrival home, our first task is to establish the colony in new quarters. For this purpose I have found a wooden box measuring about 6×6×9 inches most suitable. The box should be equipped with a glass cover in addition to the wooden one, so that the activities of the colony may be observed without difficulty. It is also desirable to replace the sides, at least in part, with fine-meshed wire screening in order to provide plenty of air. After a flight-hole has been cut near the center of one end, the bottom of the box is covered to a depth of about two inches with a layer of dry sawdust, in which a hollow is made and lined with a thick layer of cotton. Into this hollow we carefully set the comb and surround it with more cotton that will later be drawn over it by the bees. We now place a shallow porcelain dish in one of the corners of the box and fill it with diluted honey or a thin sugar solution. After we have made certain that the flight-hole is closed, we shake the colony out of the jar onto the comb and quickly put down the glass cover, over which the wooden one is then laid. We then leave the nest-box in a dark room where the bees can proceed with the work of arranging their new home. It is best not to allow the colony its liberty until the following morning, after it has been

transferred to a shady spot where it is to remain permanently. In order that the bees may easily alight and enter when returning from the field, a slanting stone is placed beneath the flight-hole, from which the cork is gently removed as soon as the colony has calmed down. On leaving the nest-box for the first time, the workers, no doubt realizing that their surroundings are not the same, take an orientation flight (cf. Chapter I), and within half an hour or so the first workers come back to the nest, laden with nectar and pollen.

During the past few years I have sometimes had more than fifty colonies under observation, most of which were kept on boards on the shady side of a partly covered, abandoned cellar. The nest-boxes of several others were placed in second and third-story windows of the Bussey Dormitory, and communicated with the outside world through holes in a board below the window screen, thus enabling me to make observations at any time during the day or night. In this way I have spent many pleasant hours, and often the activities of the bees were so fascinating that the observations were continued until long past midnight. There can hardly be any question that both at home and in summer camps a bumblebee colony furnishes a most excellent opportunity for the study of insect behavior. Doctor Edgar Anderson, who has taught natural history for a number of years in a well-known New England summer camp, informs me that there are few things in which the boys take as much interest as the intricate social life of a bumblebee colony.

CHAPTER XII

THE ECONOMIC IMPORTANCE OF BUMBLEBEES

Although bumblebees make very delicious honey, they usually store it in such small quantities, as compared with honeybees, that it would not be practicable to keep them for that purpose. However, since Darwin (1841) came to their defense ninety-three years ago, it has been shown that these industrious insects play an important, and in some cases indispensable, rôle in the pollination of many cultivated plants. While this fact is sometimes grossly exaggerated, there have also been several attempts made to minimize, or completely deny, the importance of bumblebees in the pollination of certain plants. In order to determine which of these contentions is correct, I have performed a number of experiments which throw additional light on this question. However, before these are discussed, it seems desirable to review briefly the interesting history of insect pollination.

Although it had long been known that the production of figs depends upon a small hymenopterous insect (*Blastophaga grossorum* Gravenhorst), it apparently did not occur to any of the earlier biologists that similar relations might exist between other insects and plants. Indeed in accordance with the anthropocentric viewpoint of the pre-Darwinian period, it was generally believed that the fragrance and the various forms and colors of flowers were especially created to please the human senses.

The first one who clearly recognized how essential in-

sects are for the pollination of flowering plants was the German biologist, Kölreuter (1761). This important discovery was confirmed about thirty years later by Sprengel (1793), who, in addition to greatly extending the list of insect-pollinated plants, called attention to various remarkable floral structures and mechanisms, and advanced the theory—rather startling for that time—that not only these, but the flowers themselves, are divine contrivances to insure insect pollination.

Although some of his observations were later directly or indirectly confirmed, Sprengel's "theory of flowers" was rejected by most biologists, and was in danger of being completely forgotten, when the Darwinian theory of evolution suddenly placed it in a new light. Inquiry into the relations between insects and flowers now became one of the most popular fields of research and resulted in a vast literature. After a subsequent period of comparative inactivity, the study of the ecology of insects and flowers has recently entered upon a new era which promises further important achievements for this branch of biology, notably through the work of Knoll (1921-26), and Clements and Long (1923).

In Chapter III of his "Origin of Species," Darwin (1859) makes the following statement concerning the pollination of clover by bees: "From experiments which I have tried, I have found that the visits of bees, if not indispensable, are at least highly beneficial to the fertilization of our clovers; but humble-bees alone visit the common red clover (*Trifolium pratense*), as other bees can not reach the nectar. Hence I have very little doubt, that if the whole genus of humble-bees became extinct or very rare in England . . . red clover would become very rare, or wholly disappear."

A few years later, this conjecture of Darwin was attacked by the American botanist, Thomas Meehan (1870)¹ who asserted that the fertility of clover is not dependent upon bees, or other insects, to any material extent. Probably as a result of this adverse criticism, Darwin (1876) performed additional experiments, and found that a hundred flower-heads of *Trifolium pratense* which he covered with a net did not produce a single seed, while a hundred others which were visited by bees yielded several thousand. But even this did not convince Meehan (1877), who now contended that Darwin's results were due to differences in nutrition, and not to insects. However, in 1885—three years after Darwin's death—an event occurred which convinced even such skeptics as Meehan (1893).

For many years the farmers of New Zealand, especially those of the South Island, had been obliged to import all their red clover seed, because this important forage plant would not produce seed freely in their own country, a condition which was changed almost overnight by the successful introduction of bumblebees. In addition to such indisputable confirmation, Darwin's conclusion regarding the relation of bumblebees to red clover was later also corroborated by the observations, as well as experiments, of numerous biologists.

Within the last few years, however, Darwin's views on this question have again been assailed, this time by the Austrian biologist, Heikertinger (1919), who bases his criticism on the following statement by Knuth (1898): "To be sure, bumblebees are the chief (not, as Darwin thought, the only) pollinizing agents of red clover. Nevertheless, if we exclude these, there still remain numerous

¹ For several additional papers on this subject by Meehan, cf. *American Naturalist*, Vol. 59, pp. 441-451.

normally sucking and pollen-gathering insects to bring about the cross-pollination necessary to complete fertility; therefore the link of the above chain: 'The more humble-bees, the more fertile red clover' does not hold true."

In reply to Heikertinger, it may be pointed out, first of all, that both he and Knuth overlooked the fact that Darwin later subjected this problem to further investigation, the results of which were published more than twenty years before the appearance of Knuth's criticism. In his report, Darwin very clearly sets forth his final position concerning this matter in the following words: "It is at least certain that humble-bees are the chief fertilizers of the common red clover."

But even if we disregard this oversight on the part of Knuth and Heikertinger, we are still confronted with the important question, whether or not there are plenty of insects, besides bumblebees, as Knuth maintains, which insure the complete fertility of red clover. While it is possible that Knuth's assertion may apply to a few restricted areas, there is a large body of evidence which shows conclusively that Darwin's maxim, "the more humble-bees, the more fertile red clover," is probably true of most regions of the world.

In this connection the following observations, made in the vicinity of Boston from June, 1921, to October, 1933, seem worth recording. Throughout the greater part of the summer, large numbers of bumblebees could always be found on red clover unless the weather was very inclement. Several solitary bees and a few butterflies were also sometimes encountered; but most of these visit the flowers in such a desultory fashion, as compared with bumblebees, that the red clover in the vicinity of Boston would probably set little or no seed if its pollination depended upon

PLATE VIII.



Three racemes of the hardy garden larkspur (*Delphinium cultorum*), illustrating the necessity of bumblebee pollination. The bumblebees did not have access to the flowers on raceme b and the upper part of raceme c. Slightly reduced.

insects other than bumblebees. This apparently is likewise the case with purple vetch (*Vicia cracca*), since other insects rarely come to this plant for nectar and pollen.

In regard to the honeybee, concerning whose relation to red clover there has been much controversy, it may be mentioned that during the entire course of these observations not a single individual of *Apis mellifica* was seen on *Trifolium pratense*, although quite a number of them were working on alsike (*Trifolium hybridum*) and white clover (*Trifolium repens*) which were growing near or among the red clover. However, by this statement I do not wish to imply that *Apis mellifica* may not occasionally obtain nectar and pollen from *Trifolium pratense*.

Like red clover, the hardy garden larkspur (*Delphinium cultorum* Voss) is classed as a typical bumblebee flower, for the members of the genus *Delphinium* are said to be largely, if not wholly, dependent upon bumblebees for pollination. In his work with *Delphinium consolida*, Darwin found that plants covered with a thin net produced only about half as many seeds as those to which bees had free access.

In order to determine the effect of the exclusion of bumblebees on the fertility of *D. cultorum*, I enclosed five large plants, each having quite a number of racemes in various stages of development, in one-sixteenth inch mesh wire cages, after the number of flowers and buds on each raceme had been recorded on cards. On August 25, 1923, when the experiment was started, many of the racemes were in full bloom; on others, the lower flowers had opened, while thirty-five bore only buds. When the five plants were harvested on September 29, each follicle of the racemes which were in bloom at the time they were enclosed contained an average of twenty-two seeds, as did those which had not been placed in cages. This was also

true of the lower follicles of the racemes which had just recently begun to flower, but no seeds were present in the upper follicles. On the other hand, from the thirty-five racemes which were enclosed when they were still in bud, a total of only twenty-one seeds was produced instead of 27,720 which should have been harvested, estimating at the rate of twenty-two seeds per follicle and thirty-six follicles per raceme (Pl. VIII).

It will be noticed that these results differ considerably from those of Darwin with *Delphinium consolida*, but approach very closely to what one should expect in the case of *Delphinium elatum*, which is considered by Müller (1873) and Knuth to be self-sterile. The twenty-one seeds obtained in my experiments with *D. cultorum* might very well be due to small ants, many of which were observed on the flowers of some of the enclosed racemes. A similar explanation may account for Darwin's results, although it is possible, of course, that *Delphinium consolida*, unlike *D. cultorum* and *D. elatum*, is capable of self-pollination.

In the vicinity of Boston, the flowers of *D. cultorum* are visited chiefly by bumblebees, and what is even more remarkable, almost exclusively by two species: *B. affinis* and *B. fervidus*. *Bombus fervidus* secures the nectar in the normal way, but the workers as well as the queens of *B. affinis* invariably perforate the spur, and hence very likely are of no importance in the pollination of the plant.

Late in the summer, bumblebees, other than the males and workers of *B. fervidus*, are rarely seen on *D. cultorum*. We have here, therefore, a similar state of affairs as in the case of *D. elatum*, which in certain parts of Europe is said to be wholly dependent upon *B. hortorum* for pollination.

CHAPTER XIII

CLASSIFICATION BASED ON BEHAVIOR

It is of comparatively little use to make observations on the behavior of any organism unless one knows with what species one is dealing. This is especially true in working with insects, of which over 500,000 species have thus far been described. Although bumblebees constitute less than one-tenth of one per cent of this large total, their classification offers many obstacles, chiefly because this group lacks conspicuous morphological characters, and because of the frequent convergence in coloration of species which are not closely related. What has been accomplished in bumblebee taxonomy up to the present time has been based almost exclusively on structural characters, while comparatively little attention has been paid to behavior as a means of classification. It has even been asserted that behavior is of no taxonomic value whatsoever so far as bumblebees are concerned. Wagner (1907), for instance, has the following to say in the introductory pages of his rather negativistic treatise on the psychobiology of bumblebees: "These are the facts which compel us from the very beginning to give up all hope of finding fixed and unalterable characters in the taxonomy of bumblebees for the elucidation of the behavior of these insects, and, *vice versa*, of deriving suitable data from their behavior for taxonomic purposes."

As we shall see later, this statement of Wagner is untenable. In fact, as has been recently pointed out by Frison (1925), morphological characters sometimes prove

wholly inadequate, and it is often necessary to resort to the study of behavior in order to distinguish between certain bumblebee species. Moreover, during the past fifty years, several important attempts, most of which antedate Wagner's work, have been made to subdivide the Bombidae into natural groups. These subdivisions have been based upon (1) coloration, (2) structure, or (3) habits, and in some cases on two, or on all three of these.

I shall here discuss in detail those attempts to subdivide the Bombidae into natural groups which have been made with behavior as a criterion, and subject them to a critical examination in the light of extensive observations on some of our American species. Before doing so, however, it seems desirable to review several efforts at grouping which have been made on the basis of (1) coloration and (2) structure.

The Austrian entomologist, von Dalla Torre (1882) is apparently the only one who tried to subdivide the Bombidae according to coloration. But since many species of bumblebees which are not closely related show striking similarities in coloration, as for example *B. americanorum* and *B. terricola*, this method of grouping is artificial, and for this reason has not been favorably received by other entomologists.

The first one to recognize clearly that there are two distinct structural groups of bumblebees was the English entomologist, Kirby (1802), who noticed that the females of certain species lack *corbiculae*, or pollen baskets. Illiger (1806), suspecting a corresponding difference in habit, separated the species thus characterized from the true bumblebees, and Newman (1834) later gave this new subdivision the generic name *Apathus*. This term held sway for over forty years, when it was discovered that

the name *Psithyrus* had precedence over the name *Apathus*, since it had been used somewhat earlier by Lepeletier (1832).

Since the separation of the parasitic from the true bumblebees, several attempts have been made to classify the latter on the basis of structure. The first of these attempts was by the Russian general, Radowszkowski (1884), who placed the nonparasitic species in eleven subdivisions. This system of grouping was later somewhat modified by Franklin (1912) in his "Bombidae of the New World," in which the then known eighty-five American species of the genus *Bombus* are divided into seven groups.

Another classification which has much in common with Radowszkowski's is that of Vogt (1911) who separated the genus *Bombus* into nine subgenera, which Ball (1914) and Krüger (1916 and 1920) later increased to ten and thirteen respectively. Krüger, in addition to making a few modifications in the subgenera established by Vogt, has divided the genus *Bombus* into two sections, *Odontobombus* and *Anodontobombus*, on the basis of the presence or absence of a spinous projection on the posterior, distal angle of the metatarsus of the middle legs. This character may prove of considerable importance in determining the genetic relationship of the various species of bumblebees, since, as we shall see later, it seems to be correlated with certain fundamental differences in the methods employed by these insects in feeding their larvae. In 1922, Skorikov elevated many of the subgenera established by Vogt, Ball, and Krüger to generic rank by breaking up the genus *Bombus* into nineteen genera and a large number of new subgenera. In a recent paper on the classification of our North American species, Frison (1927 c), after calling at-

tention to the weakness of Skorikov's system, points out that there is no necessity for such a "wholesale elevation" to generic status in the case of bumblebees. However, he has accepted several of Skorikov's genera as subgenera, and has erected the additional subgenus *Separatobombus*.

Another independent subdivision of the nonparasitic bumblebees based on structure is that of Robertson (1903), who removed certain species from the genus *Bombus* and erected the genus *Bombias*, chiefly on account of the unusually large eyes of the males, and the size and position of the ocelli in the females. This new genus was later reduced to subgeneric rank by Franklin, but, as has been pointed out by Frison, it deserves greater consideration than has been accorded to it up to the present time, since the structural peculiarities which caused Robertson to separate *Bombias* from the genus *Bombus* are correlated with well-defined peculiarities in behavior. Because of this, Frison has elevated the genus *Bombias* to a new section, *Boopobombus*, equal in rank with the two sections proposed by Krüger.

Among the attempts to divide the genus *Bombus* into natural groups by using structure as a criterion, we may also include that of Friese and von Wagner (1910), who constructed a "Stammbaum" which is intended to show the probable genetic relationships of the fifteen species of *Bombus* occurring in Germany. This scheme of grouping will no doubt have to be very much modified, since it is not in harmony with certain fundamental traits in behavior which have been pointed out by Sladen (1899 and 1912).

As regards the genus *Psithyrus*, Franklin later extended Radowszkowski's system to this subdivision of the Bom-

bidae by assigning our American species to three groups,¹ which Frison, "for the sake of uniformity," has recently changed to subgenera.

The first one who classified the Bombidae according to behavior was the English entomologist, Frederick Smith (1876). In the second edition of his "Catalogue of British Bees," he separated the English species into Surface-builders (Section I) and Underground-builders (Section II). While this method of dividing the genus *Bombus* may be of some value to the amateur naturalist, it is of little importance for taxonomic purposes, since certain species of bumblebees, such as *B. vagans*, make use of many diverse nesting-sites. This species has been found nesting in hollow trees, stone walls, birds' nests, attics, and even fur coats.

A more promising and dependable character for a natural grouping of the Bombidae was discovered by Sladen (1899), who called attention to the fact that certain species of bumblebees construct at the side of each mass of growing larvae little waxen pockets or pouches, into which the workers drop the pellets of pollen from their hind tibiae on their return from the field, while other species store the newly gathered pollen in waxen cells or in old cocoons, from which it is taken as required, and fed to the larvae. On the basis of this difference in the method of rearing their young, he separated the English species into Pouch-makers and Pollen-storers.

Thirteen years later, Sladen, in addition to elaborating the foregoing scheme in general, changed the term Pouch-makers to Pocket-makers, and further subdivided the

¹ My reduction of these three groups to two in an earlier publication, when I did not as yet realize the negligible taxonomic value of coloration, I now consider to be a mistake (cf. *Biol. Bull.*, Vol. 43).

latter into Pollen-primers and Carder-bees. However, shortly after this revision had appeared in print, he discovered that the character he used for distinguishing the Pollen-primers is not a reliable one, and therefore substituted "Long-faced humble-bees" as a tentative name for *B. ruderatus*, *B. hortorum*, *B. latreillellus*, and *B. distinguendus*.

The two hundred and twenty-five bumblebee colonies which I had under observation during the past thirteen years, including those reared in artificial nests, furnished an excellent opportunity to test the soundness of Sladen's classification as applied to four of the nine American subgenera of the genus *Bombus*. The results of this investigation show that Sladen's work provides an excellent basis for further taxonomic and phylogenetic work, but that certain details of his scheme will have to be modified.

As already mentioned, Sladen divided the English species into two main groups, the Pollen-storers and the Pocket-makers. Concerning the latter, Sladen says, "When the usual receptacles for pollen employed by a particular species are not available, it may adopt those employed by others. Thus in a strong nest of *B. agrorum*, one of the pocket-making species that I had under observation in 1910, the workers, during a period when there were no growing larvae and consequently no pockets for pollen, dropped all the pollen they brought home into a special waxen cell they had constructed, like *terrestris*, on the top of some cocoons. Also a colony of *B. hortorum*, another pocket-maker, being in an advanced stage, and having no growing larvae, placed pollen in the cocoons vacated by the young queens, but only lined the interior of the cocoons with it."

In connection with these statements of Sladen, I should

PLATE IX.



1. Comb of *Bombus affinis* with three pollen cylinders. Natural size.



2. Six pollen cylinders taken from a nest of *Bombus affinis*. Sometimes more than a dozen of these pollen cylinders are found in one nest. Natural size.

like to point out that *B. americanorum* and *B. fervidus*, two of our American Pocket-makers, store pollen not only under the conditions specified by him, but also at the time the young queens and males are reared, when prosperous colonies of both species sometimes accumulate considerable quantities. Thus on July 20, 1927, I dug up a colony of *B. fervidus*, consisting of the old queen and about seventy-five workers, which was in an exceptionally flourishing condition, having a large number of eggs and cocoons and many growing larvae. On the periphery of the comb were found three waxen cylinders, about an inch and a half high, and almost completely filled with pollen. It is therefore evident that Sladen's term Pollen-storers is of little use in any comprehensive classification of the Bombidae.

Furthermore, in regard to certain Pocket-makers, such as *B. americanorum* and *B. fervidus*, it is well to note that pockets are built only for those larvae which are destined to become workers, while the brood which furnishes the other two castes (queens and males) is fed by regurgitation; that is, in the same manner as the brood of all three castes of the non-pocket-making species. But since this method of feeding the male and the queen larvae is not employed by the Pocket-makers—at least in the temperate regions—until toward the end of the breeding season, and since the manner in which this group feeds its worker brood is quite distinctive, it seems best to retain the name Pocket-makers, unless future investigations show that the use of the term is impracticable.

We now come to Sladen's division of the Pocket-makers into Pollen-primers and Carder-bees. As already mentioned, Sladen later removed two species from the Pollen-primers, but the following observations clearly show that the term Pollen-primers will have to be rejected as a sub-

division of the Pocket-makers. In the fall of 1921, I made detailed observations on a large colony of *B. impatiens*, a non-pocket-making species, and found that the egg-cells were regularly primed with pollen pellets before the workers oviposited in them.

Even more unsatisfactory is the name Long-faced bumblebees, which Sladen introduced later, since *B. mendax*, which structurally belongs to an entirely different group, and probably is a non-pocket-making species, has a longer face than any of the four species mentioned by Sladen (1912).

Equally unsuitable is the term Carder-bees, by which Sladen designates the second subdivision of the Pocket-makers. The collecting of nesting-material, the character on which this group was based, is more or less common to all species of the genus *Bombus*, including the non-pocket-making species. However, by the rejection of the name Carder-bees, I do not wish to imply that the species which Sladen lists under this term may not constitute a distinct group.

Having shown the inadequacy of Sladen's classification as applied to some of our North American Bombidae, I would suggest the following changes in his scheme. The name *Marsipopoea*¹ (from Greek *marsipos*, a pouch, and *poiein*, to make) is proposed as a substitute for the term Pocket-makers. This change would result in a suitable name for Sladen's Pollen-storers (the non-pocket-making species), which could then be designated as the *Amarsipopoea*. For reasons already stated, it is further suggested that the terms Pollen-primers, Long-faced bumblebees,

¹ The names *Marsipopoea*, *Amarsipopoea*, *Cryptoschadonia*, and *Phaneroschadonia* are modifications of terms which I used in a recent paper (cf. *Biol. Bull.*, Vol. 52).

and Carder-bees be dropped as subdivisions of the *Marsipopoea*.

Concerning two species belonging to the *Amarsipopoea*, Sladen says: "The larvae of *B. terrestris* and *lucorum* do not keep together in a compact mass, but as they begin to grow large each one acquires its own covering of wax, although they do not separate completely; the cocoons, therefore, do not form definite clusters, and are easily detached from one another." And in the next paragraph he continues: "With most of the species the skin of wax that covers each batch of larvae is to the unaided eye unbroken, but as the larvae grow, *B. terrestris*, *lucorum*, and *latreillellus* leave visible holes in the wax, which, when the larvae approach full size, become large. The larvae would now run the risk of falling out of their soft wax covering, which would mean their destruction, for a naked larva is always carried out of the nest; but they avoid this danger by enclosing themselves in a loose web of silk, doing this a day or two before they begin to spin their cocoons."

What Sladen says in regard to *B. terrestris* and *B. lucorum* is also true of some of our American *Amarsipopoea*, for example *B. affinis* (Pl. XI) and *B. terricola*. Quite contrary to this treatment of the larvae is that of the other American and European *Amarsipopoea* whose habits have been studied, for these keep their larvae completely covered with wax. Because of this difference in behavior, I propose the name *Phaneroschadonia* (from Greek *phaneros*, visible, and *schadon*, a bee larva) for those *Amarsipopoea* whose larvae are partly exposed during the greater part of their development, and the name *Cryptoschadonia* (from Greek *cryptos*, hidden) for those *Amarsipopoea* which carefully enclose their larvae in a waxen envelope.

Besides the loosely connected cocoons and the exposed larvae, the *Phaneroschadonia* exhibit a number of other characteristics which mark them as a distinct group. Among these may be mentioned (1) the short antennae of the males, (2) the similarity in form between males and workers, and (3) the extreme shortness of the head. The last character is coupled with a short tongue, which makes it necessary for this group of bumblebees to perforate long-tubed flowers in order to secure the nectar.

The *Phaneroschadonia* have in addition the following characteristics: (1) they construct—usually near the center of the comb—one or more bulky, waxen tubes in which they store large quantities of pollen (Pl. IX1 and 2); (2) the wax which they produce is dark and brittle, as if mixed with black soil; and (3) their males are rather sluggish as compared with those of other *Bombus* species. It may be pointed out, furthermore, that the *Phaneroschadonia* appear early in spring, that they ordinarily do not nest on the surface of the ground, and that—as far as is known—they do not occur in South America.

However, it may be necessary to use the terms *Cryptoschadonia* and *Phaneroschadonia* provisionally, at least for the present, since Sladen states that *B. latreillellus*, a Pocket-maker (*Marsipopoea*), also leaves its larvae partly uncovered. This seems strange, for the other *Marsipopoea* studied are very careful to keep their larvae completely covered with wax (Pl. X2). The only explanation I can offer for this surprising dissimilarity is that Sladen's observations on *B. latreillellus* may have been made during extremely hot weather, when, owing to the softening of the wax, all bumblebee larvae are likely to become exposed. Should subsequent observations confirm Sladen's statement concerning *B. latreillellus*, other terms will have

PLATE X.



1. Comb of *Bombus affinis*, showing exposed larvae. Somewhat reduced.



2. Comb of *Bombus americanorum*, showing three pockets. The larvae of this species and its close relatives are completely enclosed by wax. Slightly reduced.

to be substituted for *Cryptoschadonia* and *Phaneroschadonia* to bring out the distinct character of the group of bumblebees here designated as the *Phaneroschadonia*.

As already stated, the *Cryptoschadonia*, the remaining members of the *Amarsipopoea*, can be easily separated into two groups on the basis of structure, one of which is identical with the genus *Bombias* of Robertson. Because of a lack of sufficient material, I have thus far been unable to ascertain whether the species which belong to this group have any clearly defined peculiarities in storing their food or rearing their young, but as was pointed out in Chapter III, the males of this group have the unique habit of darting after flying objects, a trait which is no doubt correlated with their unusually large eyes. I therefore propose the name *Aicarrenia* (from Greek *aissein*, to dart, and *arren*, a male), until it can be determined whether this group of bumblebees has other peculiarities which would permit of a designation more in harmony with the terms proposed for the remaining groups.

Concerning the relative temper of the *Marsipopoea* and *Amarsipopoea*, Sladen says: "It will be noticed that the pouch-makers include roughly the timid species. . . . The pollen-storers, on the contrary, consist of the bolder species." This is not true of our North American *Marsipopoea*, for example *B. americanorum* and *B. fervidus*, since they are the most vicious bumblebee species with which I have ever come in contact, while most of our *Amarsipopoea* are comparatively gentle.

It will be interesting to see whether the various groups which have been established on the basis of structure are really made up of homogeneous species when their habits are studied from a taxonomic point of view. It will also be interesting to investigate the methods which the true

bumblebees employ in feeding the larvae of the genus *Psithyrus*, since certain species of the latter, such as *Psithyrus variabilis*, breed in the nests of the *Marsipopoea*, while others, for example *Psithyrus ashtoni*, are parasitic on the *Amarsipopoea*.

The table on page 131 is a tentative classification of some of our more common North American bumblebees on the basis of behavior.

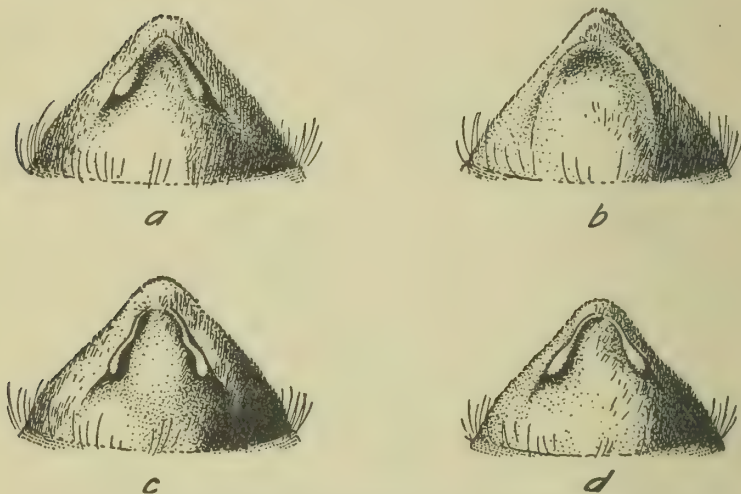


FIG. 3. Apical segments of four *Psithyrus* females showing ridges on ventral side: a, *Ps. ashtoni*; b, *Ps. fernaldae*; c, *Ps. insularis*; d, *Ps. laboriosus*. Greatly enlarged.

GENUS *BOMBUS* ¹

AMARSIPOPOEA

PHANEROSCHADONIA

1. *B. affinis* Brown-patched Bumblebee
2. *B. terricola* Brown-tailed, Yellow-banded Bumblebee

CRYPTOSCHADONIA

3. *B. bimaculatus* Yellow-patched Bumblebee
4. *B. impatiens* Yellow-notched Bumblebee
5. *B. perplexus* Shaggy, Brown-tailed Bumblebee
6. *B. ternarius* Orange-belted Bumblebee
7. *B. vagans* Shaggy, Black-tailed Bumblebee

AICARRENIA

8. *B. auricomus* Large-eyed, Yellow-banded Bumblebee
9. *B. separatus* Brown-girdled Bumblebee
10. *B. rufocinctus* Rufous-belted Bumblebee

MARSIPOPOEA

11. *B. borealis* White-faced, Amber Bumblebee
12. *B. americanorum* Black-tailed, Yellow-banded Bumblebee
13. *B. fervidus* Black-faced, Yellow Bumblebee

GENUS *PSITHYRUS* (Fig. 3)

1. *Ps. ashtoni* Host: *B. affinis* and *B. terricola*
2. *Ps. fernaldae* " not known
3. *Ps. insularis* " *B. flavifrons*
4. *Ps. laboriosus* " *B. impatiens* and *B. vagans*

¹For a comprehensive classification of both the American and European species cf. Plath, "The Natural Grouping of the Bremidae (Bombidae)," *Biol. Bull.*, Vol. 52, pp. 394-410.

APPENDIX

DETAILED ACCOUNT OF THE COMMON NORTH AMERICAN SPECIES

GENUS BOMBUS

AMARSIPOPOEA

PHANEROSCHADONIA

1. *Bombus affinis* Cresson (Fig. 4)

(Including its variety *novae-angliae* Bequaert)
Brown-patched Bumblebee

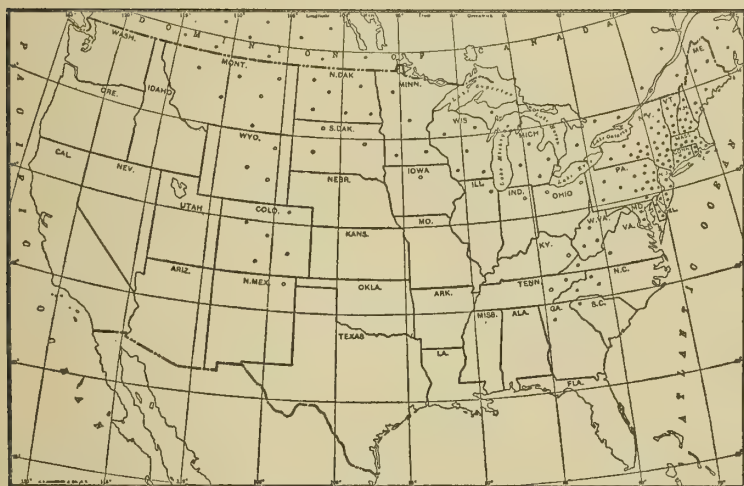


FIG. 4. Geographical distribution of *Bombus affinis*. Dots indicate known range, and circles, probable range.

A. Coloration and Approximate Size:

QUEEN: black, with thorax and first two abdominal segments yellow.

WORKER: usually with a black interalar band. The second abdominal segment almost entirely brown.

MALE: colored like the worker, except that the top of the head bears yellow pile.

The pile of this species is short and thick.

In normally colored specimens of *B. affinis*, the differences between queen and worker are more marked than is usual among bumblebees, so much so that Franklin (1912) was at first in doubt that they were conspecific. As stated above, the workers and males generally have a black interalar band, and brown pile on the second segment, while in the normally colored queen the pile on the thorax and first two abdominal segments is pure yellow. Occasionally, however, one finds queens that present one or the other, or both of these characteristics of the other two castes.

A color variant of this species, variety *novae-angliae* Bequaert, has the fourth abdominal segment covered with rufous hairs (cf. *Bull. Mus. Comp. Zoöl.*, Vol. 67, p. 278).

The normally colored queens of *B. affinis* are sometimes confused with those of *B. perplexus* and *B. vagans*. *B. perplexus* may be distinguished from both *B. affinis* and *B. vagans* by the tawny shade of its yellow pile, and by the brownish hairs on the sixth segment and on the apical margin of the fifth. *B. vagans* differs from *B. affinis* by its long and shaggy pile. The queens of *B. affinis* are among the largest of our New England bumblebees, and those of *B. vagans* never even nearly approach them in size.

QUEEN: length, 20 mm.; wing expanse, 40 mm.

WORKER: " 12 " " " 30 "

MALE: " 12 " " " 30 "

B. Life-cycle:

In the vicinity of Boston, the queens of *B. affinis* begin to appear about the middle of April, but in the exceptionally early spring of 1925, a queen of this species was seen on April 7. Most colonies are probably started in May. The workers are usually quite common by the first week in June, and the males and young queens are produced largely in August and September. The more prosperous colonies do not break up until October.

C. Nests:

During the years 1921-1933, 66 nests of this common New England species were discovered, 36 of which were transferred to nest-boxes for further study. All were subterranean, and those taken were situated from 1 to 4 feet below the surface of the ground, with tunnels varying from 18 inches to 8 feet in length. The colonies of this species are usually quite populous, a nest taken September 1, 1922, containing 19 young queens, 27 males, and 175 workers.

D. Favorite Flowers:

The queens of *B. affinis* are particularly fond of rhododendron and the flowers of the barberry and horse-chestnut, while the workers are often found in large numbers on rhododendron, mountain laurel, rose, St. John's-wort (*Hypericum*), larkspur, jewel-weed (*Impatiens*), and butter-and-eggs (*Linaria*). The nectar of long-tubed flowers is obtained by perforation of the corolla. The males may usually be seen sipping nectar on milk-weed, sumac, button-bush (*Cephalanthus*), sweet pepperbush (*Clethra*), and boneset (*Eupatorium*).

E. General Remarks:

B. affinis is comparatively gentle in disposition. When a nest is disturbed, the workers returning from the field immediately fly away, as a rule, as soon as they notice the intruder.

As has been pointed out in the first part of this book, *B. affinis* is heavily parasitized by *Ps. ashtoni*, 11 of the 36 nests taken being infested by this *Psithyrus*, and the queens of *B. affinis* in turn frequently parasitize incipient colonies of *B. terricola*.

2. *Bombus terricola* Kirby (Fig. 5)

Brown-tailed, Yellow-banded Bumblebee



FIG. 5. Geographical distribution of *Bombus terricola*.

A. Coloration and Approximate Size:

QUEEN: head black. Thorax yellow in front and black behind. The second and third abdominal segments are yellow, the remaining ones black, and the tip of the abdomen bears a brown fringe.

WORKER: colored like the queen.

MALE: face and head yellow. The sixth and seventh abdominal segments usually with a considerable amount of brown pubescence.

The pile of this species is of medium length and rather fine.

B. terricola closely resembles *B. americanorum* and *B. auricomus* in coloration. From the latter it can be distinguished by its much smaller size. The queens and workers of *B. terricola*

can be differentiated from those of *B. americanorum* by the brown pile on the tip of the abdomen; the males by the yellow pile on the face, which is gray in the males of *B. americanorum*. In the latter, yellow often occurs on the fifth and sixth abdominal segments, but in those of *B. terricola* this is never the case.

QUEEN: length, 16 mm.; wing expanse, 38 mm.

WORKER: " 12 " " " 30 "

MALE: " 12 " " " 30 "

B. Life-cycle:

B. terricola is one of the first bumblebees to appear in spring—my earliest record is April 6. Most colonies are started toward the end of April. The workers begin to appear shortly after the middle of May, and the males and young queens are produced chiefly in July and August.

C. Nests:

Of this species, which is somewhat less common in the vicinity of Boston than *B. affinis*, 20 nests were discovered, 14 of which were taken. One of these was found among some old straw in a box left in an abandoned greenhouse, while the remaining 13 of the 19 subterranean nests were situated from 6 to 18 inches below the ground, and had entrance tunnels ranging from about 6 inches to 3 feet in length. Most of the colonies did not average more than 50 bees, but four were considerably larger. One, taken on July 12, 1923, consisted of the old queen, over 50 young queens, and more than 150 workers, besides a large number of cocoons, which were interspersed with about a dozen pollen cylinders, similar to those frequently found in the nests of *B. affinis*. These cylinders contained more than a quarter of a pound of pollen. The wax of this species, like that of *B. affinis*, is unusually dark and brittle, as if mixed with black soil.

D. Favorite Flowers:

The queens of this species are frequently seen on willow, crocus, gooseberry, barberry, rhododendron, and mountain

laurel, while the workers visit chiefly rhododendron, honeysuckle (*Diervilla*), mountain laurel, rose, white clover, basswood, and purple vetch. Both the queens and workers perforate long-tubed flowers in order to obtain the nectar, as do those of *B. affinis*. The males are fond of milkweed, basswood, sumac, sweet pepperbush, and boneset.

E. General Remarks:

B. terricola, like *B. affinis*, is parasitized by *Ps. ashtoni*, but I have found this *Psithyrus* breeding in only 2 out of the 14 nests of *B. terricola* which I have taken. However, the observations of Professor O. A. Stevens of North Dakota Agricultural College and of Mr. G. B. Fairchild, who has collected extensively in northern Nova Scotia, seem to indicate that *B. terricola* is more heavily parasitized in parts of the United States and Canada where *B. affinis* is absent or rare.

B. terricola is somewhat more vicious than *B. affinis*. During the summer of 1920, I accidentally discovered 2 nests of *Bombus occidentalis*, a close relative of *B. terricola*, at Berkeley, California (cf. Plath, 1922c). One of these, dug up on the University of California campus on July 12, 1920, contained 5 young queens and over 80 workers. This colony was transferred to an observation box, but was destroyed shortly afterwards by Argentine ants (*Iridomyrmex humilis* Mayr). The workers of *B. occidentalis* are somewhat larger and even more vicious than those of *B. terricola*.

CRYPTOSCHADONIA

3. *Bombus bimaculatus* Cresson (Fig. 6)

Yellow-patched Bumblebee



FIG. 6. Geographical distribution of *Bombus bimaculatus*.

A. Coloration and Approximate Size:

QUEEN: black, with thorax and first abdominal segment yellow; the basal middle of the second segment with a somewhat crescent-shaped patch of yellow pile.

WORKER: colored like the queen.

MALE: colored like the queen, except that the face and head bear considerable yellow pile. Occasionally one finds a male with yellowish pile on the fourth and fifth segments.

The pile of this species is of medium length and rather coarse.

A queen and 2 males taken at Forest Hills have the second and third segments covered with bright rufous pile. Another

queen, captured while she was searching for a nesting-site, has a broad black interalar band, and only a few yellow hairs on the second segment (cf. *Bull. Mus. Comp. Zool.*, Vol. 67, No. 6).

The amateur is likely to confuse *B. bimaculatus* with *B. separatus* and *B. impatiens*. *B. separatus* may be distinguished by the brown pile on the basal middle of the second segment, while the corresponding region in *B. bimaculatus* is yellow. *B. impatiens* differs from *B. bimaculatus* and *B. separatus* by the absence of light pile on the second segment, and, what is even more characteristic, by a distinct notch in the yellow pile on the apical margin of the first. It may also be pointed out that the wings of *B. separatus* are noticeably darker than those of *B. bimaculatus* and *B. impatiens*.

QUEEN:	length,	18 mm.;	wing expanse,	38 mm.
WORKER:	"	II	"	"
MALE:	"	II	"	"

B. Life-cycle:

The queens of this species begin to appear about the same time as those of *B. terricola*, *i.e.* about the middle of April—my earliest record is April 7. The workers are fairly common by the end of May, while the males and young queens are produced chiefly in June and July. Like *B. pratorum* in Europe, *B. bimaculatus* completes its life-cycle very early, and therefore one rarely encounters this species after August 1.

C. Nests:

Of this common Eastern species, 37 nests were discovered, all but 3 of which were taken. Two were found in stone walls, and 9 on the surface of the ground. The remaining 23 of the 26 subterranean nests were situated from 6 inches to 1 foot below the surface, and had tunnels varying from 9 inches to 4 feet in length. One of the shorter-tunneled subterranean nests and 2 or 3 of the surface nests were almost completely destroyed by the larvae of the tachinid fly, *Brachycoma sarcophagina*. The colonies of *B. bimaculatus* are rather small, as a rule, the

largest nest taken containing the old queen, 23 young queens, about 60 workers, and several cocoons from which the young had not yet emerged.

D. Favorite Flowers:

The queens of this species are usually found on willow, crocus, buffalo currant (*Ribes aureum*), Pedicularis, Diervilla, and rhododendron. The workers are especially fond of rhododendron, mountain laurel, honeysuckle, red clover, purple vetch, basswood, and pickerel weed, while the males may be seen on a large number of flowers, among them mountain laurel, honeysuckle, clover, vetch, basswood, and purple loosestrife.

E. General Remarks:

Although one frequently finds females of *Ps. laboriosus* in the nests of *B. bimaculatus*, they apparently never breed in them, but, as was pointed out in Chapter V, merely use them as a sort of hotel.

As has already been mentioned in Chapter III, males of this species may often be seen in June and July following each other in leisurely flight from bush to bush in search of a mate.

B. bimaculatus is rather waspish in disposition.

4. *Bombus impatiens* Cresson (Fig. 7)

Yellow-notched Bumblebee



Fig. 7. Geographical distribution of *Bombus impatiens*.

A. Coloration and Approximate Size:

QUEEN: black, with thorax and first abdominal segment covered with yellow pile, the apical margin of which is notched in the middle.

WORKER: colored like the queen.

MALE: colored like the queen, except that the face and head bear considerable yellow pile.

The pile of this species is rather short and coarse.

B. impatiens resembles *B. separatus* and *B. bimaculatus* in coloration. The distinguishing characters have been pointed out in connection with *B. bimaculatus*.

QUEEN: length, 19 mm.; wing expanse, 39 mm.

WORKER: " 12 " " " 29 "

MALE: " 12 " " " 29 "

B. Life-cycle:

In the vicinity of Boston, the queens of *B. impatiens* begin to leave their *hibernacula* about April 15, but most of the colonies are started in May. As a rule, the workers appear about the first of June, and the majority of the young queens and males emerge in August and September. Sometimes this species may be seen as late as October 15.

C. Nests:

During the years 1921-1933, 80 nests of this common American species were found, 49 of which were transferred to nest-boxes for further study. All were subterranean, and those taken were situated from 1 to 3 feet below the surface of the ground, and had entrance tunnels ranging from 18 inches to 9 feet in length.

The colonies of *B. impatiens* are usually very populous. A nest taken on August 4, 1921, contained an old dead queen, over 450 workers, and a large quantity of brood, which included at least 500 male and queen cocoons.

D. Favorite Flowers:

The queens of *B. impatiens* are frequently seen on crocus, Pieris, rhododendron, barberry, and mountain laurel; the workers on rhododendron, mountain laurel, rose, clover, purple vetch, pickerel weed, purple loosestrife, buttonbush, jewel-weed, beggar's ticks, and goldenrod. The males seem to be especially fond of boneset, goldenrod, burdock, and asters.

E. General Remarks:

The colonies of this species are sometimes parasitized by *Ps. laboriosus*, 7 of the 49 nests taken being infested.

B. impatiens is one of the more vicious of our bumblebees.

5. *Bombus perplexus* Cresson (Fig. 8)

Shaggy, Brown-tailed Bumblebee

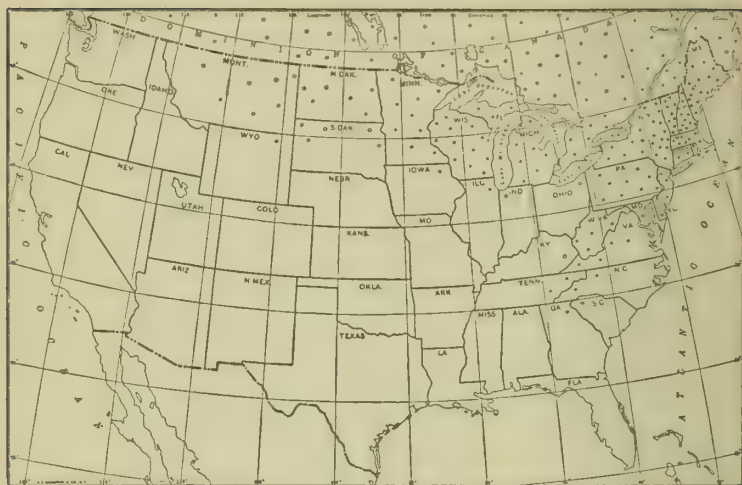


FIG. 8. Geographical distribution of *Bombus perplexus*.

A. Coloration and Approximate Size:

QUEEN: black, with thorax and first two abdominal segments tawny-yellow, the tip of the abdomen bearing brownish pile.

WORKER: colored like the queen, except that its light pile is sulphur-yellow.

MALE: face covered with yellow pile. The first three abdominal segments are sulphur-yellow, the remaining ones usually black, but sometimes partly, or even entirely yellow.

Pile rather long and fine.

This species is sometimes confused with *B. affinis* or *B. vagans*. The distinguishing characters are discussed under *B. affinis*.

QUEEN: length, 19 mm.; wing expanse, 39 mm.

WORKER: " 12 " " " 29 "

MALE: " 12 " " " 29 "

B. Life-cycle:

My earliest record for the queens of this species is April 12. Most nests are probably started in May, and the first workers are sometimes seen during the last week of that month, while the males and young queens are produced chiefly in June and July. The colonies of *B. perplexus*, like those of *B. bimaculatus*, break up rather early, so that one rarely meets with this species after August 15.

C. Nests:

Five nests belonging to this comparatively rare New England species were discovered during the summers of 1925, 1927, and 1930. All were subterranean. The first, taken July 3, 1925, was situated under a large root of a tree, and had a tunnel 2 feet long. The colony consisted of 22 workers, 1 male, and some brood, from which additional males hatched later.

The second nest, taken on July 23, 1925, was about 6 inches below the surface of the ground. It contained 9 young queens, 2 of which had recently died, 1 dead male, and 357 empty cocoons, showing that this must have been a prosperous colony earlier in the year.

The third nest, with a tunnel about 5 feet long, was discovered on June 10, 1927, in the cool sand of a shady, grass-covered bank, about 3 feet below the surface. The colony was in a flourishing condition, and consisted of the old queen, 35 workers, and a large quantity of brood. It later increased considerably in size and produced more than 50 young queens. Nests 4 and 5 were not dug up.

D. Favorite Flowers:

The queens of *B. perplexus* seem to be especially fond of rhododendron, buffalo currant, and honeysuckle. I have seen the workers on rhododendron, mountain laurel, raspberry, basswood, honeysuckle, and yellow-wood (*Cladrastis lutea*), and the males on sweet pepperbush.

E. General Remarks:

Regarding the disposition of *B. perplexus*, Franklin says: "This is the gentlest and least ready to sting of all the bumble-bee species which I have had to deal with in the living condition. This seems peculiar, as *B. vagans*, which seems to be its nearest ally, is exceedingly ferocious." This agrees with my own observations, except that I have found *B. vagans* to be just as gentle as *B. perplexus*.

6. *Bombus ternarius* Say (Fig. 9)

Orange-belted Bumblebee



FIG. 9. Geographical distribution of *Bombus ternarius*.

A. Coloration and Approximate Size:

QUEEN: head black. Thorax yellow, with a broad black interalar band. The first and fourth abdominal segments yellow, the second and third orange, and the remaining ones black.

WORKER: colored like the queen.

MALE: colored like the queen, except that the face and head are covered with yellow pile.

The pile of the queens and workers is coarse and medium in length, but that of the males is somewhat longer.

QUEEN: length, 15 mm.; wing expanse, 33 mm.

WORKER: " 10 " " " 23 "

MALE: " 10 " " " 23 "

B. Life-cycle:

The queens of *B. ternarius* are among the first to appear in spring—my earliest record is April 5. I have seen workers of this species late in May, but most of the males and young queens are probably not produced until August and September.

C. Nests:

I have taken only one nest of *B. ternarius*. Early in September, 1923, Professor C. T. Brues of Harvard University called my attention to the fact that a nest of this beautiful species had been discovered on his estate near Petersham, Mass. The nest, taken on September 15, after much digging, had a tunnel 6 feet long, and was situated about 2 feet below the surface of the ground, among some trees near a red clover field. It contained 23 young queens, 16 males, over 100 workers, and a large quantity of brood, with more than 75 young queens still in their cocoons. The colony was transferred to the Bussey grounds, where it prospered for over a month, and, probably as a result, *B. ternarius*, which is exceedingly rare in the vicinity of Boston, was fairly common in the Arnold Arboretum in 1924 and 1925.

D. Favorite Flowers:

I have seen the queens of this species on willow, Pieris, rhododendron, rose, and red clover; the workers on rhododendron, rose, clover, basswood, and purple loosestrife; and the males on sweet pepperbush and golden rod.

According to Professor W. M. Wheeler, *B. ternarius* is common in the Litchfield Hills of Connecticut and the Berkshires of Massachusetts, and there visits Eupatorium, butter-and-eggs, and various species of goldenrod.

E. General Remarks:

My experience with the colony taken at Petersham, and one reared in captivity, has convinced me that *B. ternarius* is rather waspish in disposition.

7. *Bombus vagans* Smith (Fig. 10)

Shaggy, Black-tailed Bumblebee

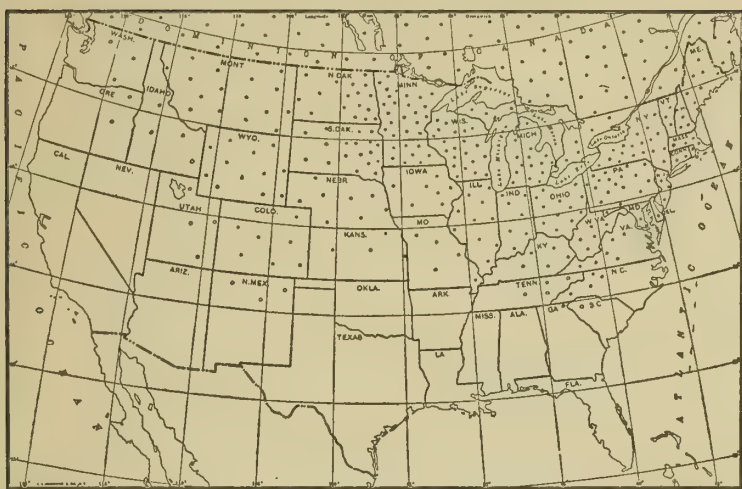


FIG. 10. Geographical distribution of *Bombus vagans*.

A. Coloration and Approximate Size:

QUEEN: black, with thorax and first two abdominal segments yellow.

WORKER: colored like the queen.

MALE: colored like the queen, except that the face and head bear considerable yellow pile.

Pile long and shaggy.

This species is rather variable in coloration. In some specimens, only the basal portion of the second segment is yellow, while in others the extreme side margins of the third and fourth as well as the entire fifth segment are covered with yellow pile. In some males, yellow may also occur on the third segment, and in others, even on the fifth and sixth.

B. vagans is sometimes confused with *B. affinis* and *B. perplexus*. For differences in the coloration of these three species see *B. affinis*.

QUEEN:	length, 16 mm.;	wing expanse, 34 mm.				
WORKER:	"	11	"	"	"	24
MALE:	"	11	"	"	"	24

B. Life-cycle:

Although the queens of *B. vagans* usually do not leave their *hibernacula* until May, a queen of this species was seen as early as April 19, in 1927. Most nests are probably started during the latter part of May. The workers begin to appear the first or second week in June, while the majority of the young queens and males are produced in August and September.

C. Nests:

Of this species, which is fairly common in the vicinity of Boston, 20 nests were discovered, 15 of which were transferred to nest-boxes for further study. Six were surface nests, and the rest subterranean. Of the latter, 9 were dug up. These were situated from 6 inches to 2 feet below the surface of the ground, and had entrance tunnels varying from 1 to 5 feet in length. The largest colony, taken August 2, 1921, consisted of the old queen, over 70 workers, and a considerable quantity of brood.

D. Favorite Flowers:

The queens of this species are usually found on rhododendron, honeysuckle, and *Pedicularis*, and the workers on mountain laurel, *Diervilla*, red clover, purple vetch, and *Baptisia*. The males seem to be especially fond of boneset.

E. General Remarks:

Four of the 15 colonies taken were parasitized by *Ps. laboriosus* variety *citrinus*, and a fifth was victimized later.

B. vagans, like *B. perplexus*, is comparatively gentle in disposition.

AICARRENIA

8. *Bombus auricomus* Robertson (Fig. 11)

Large-eyed, Yellow-banded Bumblebee

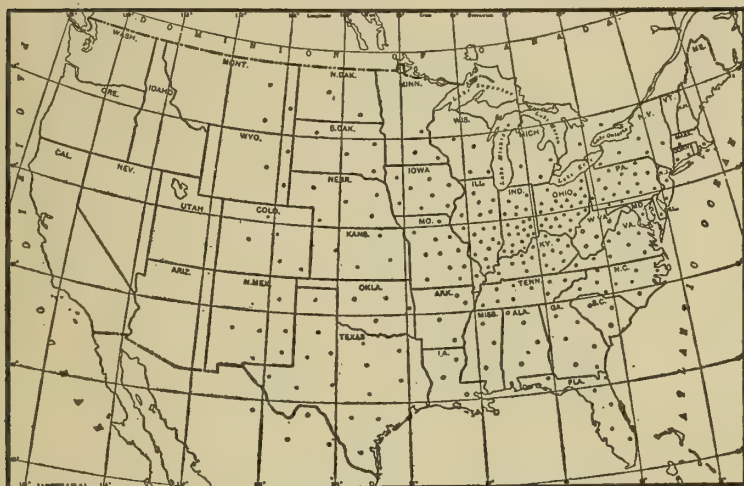


FIG. 11. Geographical distribution of *Bombus auricomus*.

A. Coloration and Approximate Size:

QUEEN: head black. Thorax yellow in front and dark behind. The second and third abdominal segments yellow, the others black.

WORKER: colored like the queen.

MALE: face and head covered with yellow pile. Thorax yellow with a poorly defined black interalar band. The second and third segments, and usually also the first, are covered with yellow pile. The remainder of the abdomen is black.

B. auricomus resembles *B. terricola* and *B. americanorum* in coloration. The distinguishing characters will be found under *B. terricola*.

QUEEN:	length, 22 mm.;	wing	expanse, 45 mm.		
WORKER:	"	17	"	"	40 "
MALE:	"	17	"	"	40 "

B. Life-cycle:

This species apparently does not occur in the vicinity of Boston.

C. Nests:

B. auricomus is rather common in some of the Middle Western States. Doctor T. H. Frison (1921) records the taking of 2 nests, one situated $1\frac{1}{2}$ feet below the surface of the ground, and the other in a hollow cement block in the foundation of a small cabin. Neither of these colonies was very populous.

D. Favorite Flowers:

B. auricomus probably frequents flowers similar to those visited by *B. separatus*.

E. General Remarks:

According to Dr. Frison, *B. auricomus* is rather mild-tempered.

9. *Bombus separatus* Cresson (Fig. 12)

Brown-girdled Bumblebee

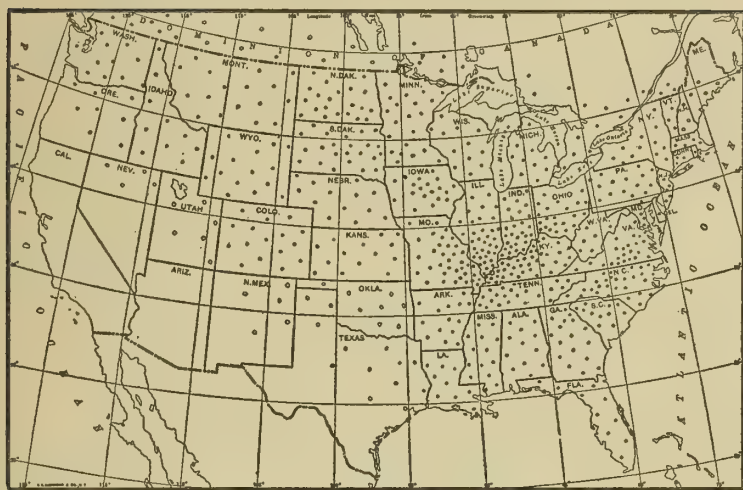


FIG. 12. Geographical distribution of *Bombus separatus*.

A. Coloration and Approximate Size:

QUEEN: black, with thorax and first abdominal segment yellow, the basal middle of the second segment brown.

WORKER: colored like the queen, except that the second segment is sometimes almost entirely brown.

MALE: the face and head are covered with yellow pile, otherwise the coloration is much like that of the worker.

Pile short and rather coarse.

A color variant of this species, variety *nero*, has considerable rufous pile on the fourth segment.

B. separatus is sometimes confused with *B. bimaculatus* and *B. impatiens*. These species have been compared under *B. bimaculatus*.

QUEEN:	length, 20 mm.;	wing expanse, 42 mm.
WORKER:	" 15 "	" " 35 "
MALE:	" 15 "	" " 35 "

B. Life-cycle:

My earliest record for the queens of this species is May 13. The workers usually begin to appear shortly after the first of June, and most of the males and young queens are probably produced in August.

C. Nests:

I have taken 3 nests of this species, which is rather common in our Southern and Middle Western States, but comparatively rare in the vicinity of Boston. All three were surface nests. One of them was discovered on July 26, 1923, after having been destroyed, probably by a skunk. Among the scattered débris were found 3 living workers, and the dead bodies of the old queen, 2 young queens, and a fourth worker. The marauder had also left behind about 100 empty cocoons, to which were attached 2 egg-cells, 1 containing 2 eggs, and the other, 5.

The second nest, taken on June 23, 1924, contained the queen, 10 cocoons, a considerable number of larvae and eggs, and 2 honey-pots with a common wall. Two other peculiarities of the double honey-pot in this nest were (1) that its walls were about twice as thick as those of the single pot usually found in incipient nests of *B. impatiens* and *B. vagans*; and (2) that it was completely closed at the time the nest was taken, whereas the queens of the other two species mentioned apparently never close their honey-pot.

The third nest, taken July 11, 1932, contained about 20 workers, 1 male, and a small quantity of brood.

Professor Joseph Bequaert of Harvard University has kindly furnished me with data concerning a nest belonging to this species which he took on July 12, 1918, at Orient, Long Island. This nest was situated in a log on the seashore, and contained

the old queen and about a dozen workers, in addition to the comb.

D. Favorite Flowers:

I have seen the queens on rhododendron, *Pedicularis*, buffalo currant, rose, red clover, and purple vetch; the workers on rose, red clover, purple vetch, basswood, and milkweed. The males seem to be especially fond of purple loosestrife and boneset.

E. General Remarks:

As has been pointed out in Chapter III, the males of this species have the interesting habit of perching on tree trunks or stalks of grass, from which they dart after passing insects in their search for a mate.

In regard to the disposition of *B. separatus*, Putnam (1864) says: "This species is nearly as ferocious, on being disturbed, as *B. ternarius*," a statement which is confirmed by my own experience.

10. *Bombus rufocinctus* Cresson (Fig. 13)

Rufous-belted Bumblebee



FIG. 13. Geographical distribution of *Bombus rufocinctus*.

A. Coloration and Approximate Size:

QUEEN: head black. Thorax yellow, a black interalar band present in some specimens. The first abdominal segment and the basal middle of the second, yellow. Yellow also occurs on the apical portion of the fourth segment and on the sides of the fifth. Several varieties have considerable rufous pile on one or more of the first four segments.

WORKER: colored like the queen.

MALE: face and head covered with yellow pile. The first and second abdominal segments are yellow, the third and fourth rufous, and the remaining ones usually yellow.

QUEEN: length, 16 mm.; wing expanse, 35 mm.

WORKER: " 12 " " " 30 "

MALE: " 12 " " " 30 "

B. Life-cycle:

Like *B. auricomus*, this common Western species does not seem to occur in the vicinity of Boston.

C. Nests:

Comparatively little is known about the nesting habits of *B. rufocinctus*. Franklin states that Putnam took a nest of this species at Bridport, Vt., in September, 1863. It was situated under the clapboards of a house, about 8 feet from the ground, and contained 28 adult bees and 35 cells with young.

D. Favorite Flowers:

B. rufocinctus probably frequents flowers similar to those visited by *B. auricomus* and *B. separatus*.

E. General Remarks:

According to Putnam, *B. rufocinctus* is one of the more savage species.

MARSIPOPOEA

11. *Bombus borealis* Kirby (Fig. 14)

White-faced, Amber Bumblebee



FIG. 14. Geographical distribution of *Bombus borealis*.

A. Coloration and Approximate Size:

QUEEN: face and head covered with yellowish-white pile. Thorax amber-yellow with a broad black interalar band. The first four abdominal segments amber-yellow, the remaining ones black.

WORKER: colored like the queen.

MALE: colored like the queen, except for the fifth abdominal segment, which is black in some specimens, amber in others, and sometimes covered with pile of both colors, in varying proportions. The legs bear more or less light pile.

B. borealis is similar in coloration to *B. fervidus*. It differs

from the latter by having yellowish-white, instead of black hairs on the face, and also by a more pronounced orange tinge of the yellow pile.

QUEEN: length, 18 mm.; wing expanse, 38 mm.

WORKER: " 13 " " " 30 "

MALE: " 13 " " " 30 "

B. Life-cycle:

I have seen only seven living specimens of *B. borealis*, all of which were queens. The dates are as follows: 4 in 1922 (May 29, June 6, July 2, July 8); 1 in 1925 (June 10); and 2 in 1927 (June 28). The queens observed in May and June apparently had but recently left their winter quarters, since they were only collecting nectar, while those encountered in July were either searching for a nest-site, or collecting pollen. These data suggest that the queens of *B. borealis*, like those of its close European relative, *B. distinguendus*, appear rather late in spring. Since in all late-appearing species the sexual forms are apparently not produced until August and September, *B. borealis* is probably no exception to the rule.

C. Nests:

The *borealis* queen seen on July 8, 1922, was eagerly searching for her nest near a stump in a hayfield, shortly after the grass had been cut. She was heavily laden with pollen, and repeatedly rose into the air to take her bearings. Whenever she alighted, she hurriedly crept about among the grass, at times frantically shaking her wings. I removed all the cut grass within a radius of about 10 feet of the stump, but even then she was unable to find her nest. Fearing that she might finally give up her search, I captured her for use in breeding experiments which have been described in Chapter X. Although I carefully examined the ground near the stump, no surface nest could be found, and it is therefore probable that the nest was subterranean.

D. Favorite Flowers:

I have seen the queens of *B. borealis* on the following flowers: Diervilla, honey locust, yellow-wood, larkspur, and purple vetch.

E. General Remarks:

Although it has not been definitely determined, *B. borealis* is probably a *Pocket-maker*.

12. *Bombus americanorum* Fabricius (Fig. 15)

Synonym: *pennsylvanicus* De Geer

Black-tailed, Yellow-banded Bumblebee

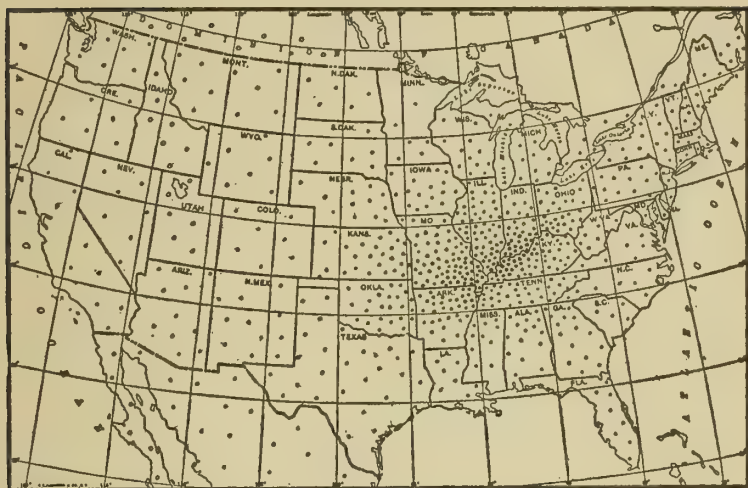


FIG. 15. Geographical distribution of *Bombus americanorum*.

A. Coloration and Approximate Size:

QUEEN: head black. Thorax yellow in front and black behind. The first abdominal segment is occasionally entirely yellow, but usually has black pile on the anterior portion. The second and third segments are yellow, the others entirely black.

WORKER: colored like the queen.

MALE: face covered with dark grayish pile. Thorax like that of the queen. The first four abdominal segments bear yellow pile; the fifth and sixth are variable, and may be yellow, black, or brown. The tip of the abdomen sometimes has a ferruginous tinge.

B. americanorum resembles *B. terricola* and *B. auricomus* in coloration. The three are compared under *B. terricola*.

QUEEN:	length,	22 mm.;	wing	expanse,	45 mm.
WORKER:	"	17	"	"	40 "
MALE:	"	17	"	"	40 "

B. Life-cycle:

In the vicinity of Boston, *B. americanorum* is comparatively rare and among the last to appear in spring. My earliest record for queens is May 27, and for workers, June 25. Most nests are probably started in May and June, and the males and young queens reared chiefly in August and September.

C. Nests:

A nest of this common North American species, which is rather rare in New England, was discovered in an open field on July 30, 1923. It was situated about 6 inches below the surface, and had a tunnel about a foot long. In it were found the old queen, 37 workers, and a considerable quantity of brood. The queen of this colony had only 1 antenna, but this apparently did not interfere greatly with her duties, for she continued to lay eggs throughout the month of August.

In the Middle West, where *B. americanorum* is especially abundant, numerous nests belonging to this species have been taken by Dr. Theodore H. Frison (1930).

D. Favorite Flowers:

I have seen the queens of *B. americanorum* on Diervilla, rose, honey locust, red clover, purple vetch, and larkspur; the workers on St. John's wort, red clover, purple vetch, and Baptisia; and the males on red clover and larkspur.

E. General Remarks:

In the Middle West, *B. americanorum* is parasitized by *Ps. variabilis*, a species which does not occur in this part of North America.

The males of *B. americanorum* may sometimes be seen flying from one prominent herbaceous plant to another in search of a mate (cf. Chapter III).

According to Frison (1918), Ranslow (cf. Howard, 1918), and Rau (1924), *B. americanorum* is rather vicious, a fact which was painfully impressed upon several of my friends shortly after the colony taken in 1923 was transferred to the grounds of the Bussey Institution. Indeed, it was necessary to remove it to another place, since the workers attacked anyone venturing within 25 feet of the nest.

13. *Bombus fervidus* Fabricius (Fig. 16)

Black-faced, Yellow Bumblebee



FIG. 16. Geographical distribution of *Bombus fervidus*.

A. Coloration and Approximate Size:

QUEEN: yellow, with a black interalar band; face and segments 5 and 6 black.

WORKER: colored like the queen.

MALE: colored like the queen, except that the abdomen has 5 segments yellow, the light pile sometimes extending onto the basal middle of the sixth.

Pile of medium length and rather coarse in texture.

B. fervidus is sometimes confused with *B. borealis*. The differences in coloration between the two have been pointed out in connection with *B. borealis*.

QUEEN: length, 20 mm.; wing expanse, 40 mm.

WORKER: " 14 " " " 32 "

MALE: " 14 " " " 32 "

B. Life-cycle:

The queens of *B. fervidus*, like those of *B. americanorum*, leave their *hibernacula* rather late in spring—my earliest record is May 6. Most nests are probably started after the middle of May. The workers usually begin to appear during the first week in June, while the males and young queens are produced largely in August and September.

C. Nests:

Of this common American species, 49 nests were discovered, all but 3 of which were taken. Two were found in stone walls, 1 under the eaves of a shed, 16 were surface nests, and the remaining 30 were subterranean, situated from 6 inches to 1 foot below the surface, with tunnels varying from 6 inches to 2 feet in length. Franklin states that the nests of *B. fervidus* never contain a large number of bees, and that the most populous colony taken by him consisted of only 47 individuals, 37 of which were workers. But evidently not all colonies of this species are small, for 7 of the 46 nests which I took contained each from 100 to 125 workers, and later more workers were produced, as well as numerous queens and males.

When one of the large *fervidus* colonies was discovered in the summer of 1921, I was at first under the impression that I was dealing with a surface nest, for a considerable quantity of nesting-material, which harbored about a dozen workers, covered the opening of the tunnel. I have since found that this is not infrequently the case with populous, subterranean nests of this species. In Europe, Hoffer (1882), Härter (1890), and Bachmann (1915) report that nests of *B. pomorum* have a similar "Vornest" or "Scheinnest." The only plausible explanation for these pseudo-nests seems to be that more nesting-material is gathered by the colony than the nest-cavity can hold.

D. Favorite Flowers:

The queens are usually seen on the pea tree (*Caragana*), on buffalo currant, rose, red clover, honey locust, and purple

vetch; the workers on red clover, rose, honey locust, larkspur, pickerel weed, purple vetch, and butter-and-eggs. The males seem to be especially fond of red clover, larkspur, and butter-and-eggs.

E. General Remarks:

As has been pointed out in Chapter VII, the workers of *B. fervidus* have the interesting habit of expelling certain intruders from their nest by daubing them with honey.

Concerning the temper of *B. fervidus*, Putnam says: "This . . . species . . . is of quite a gentle disposition, allowing its nests to be disturbed for some time before it makes any show of resistance, merely exhibiting its uneasiness by buzzing." I cannot subscribe to this statement. Of all the species with which I have had experience—including *B. terrestris*, *B. lapidarius*, *B. agrorum*, *B. muscorum*, *B. sylvarum*, and *B. helferanus* in Europe—I have found *B. fervidus* and its close relative *B. americanorum* to be by far the most vicious. Usually, when their nest is disturbed, several workers at once pounce on the intruder and punish him, and if he takes to his heels, they may in their vindictiveness pursue him for a hundred yards or more.

GENUS *PSITHYRUS*

1. *Psithyrus ashtoni* Cresson (Fig. 17)

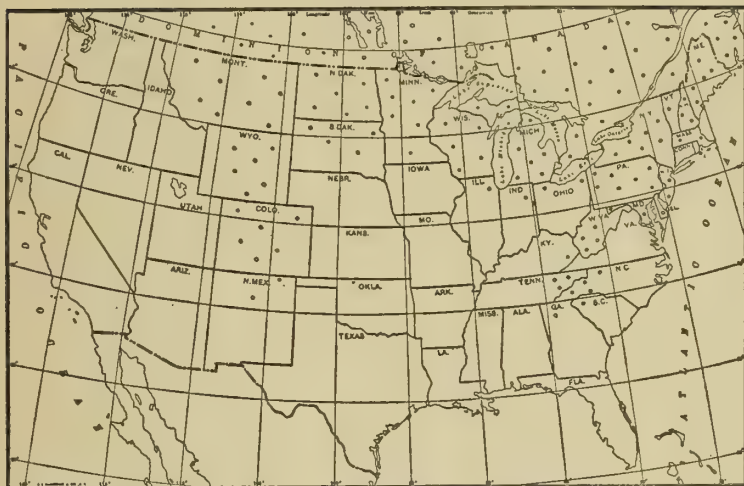


FIG. 17. Geographical distribution of *Psithyrus ashtoni*.

A. Coloration and Approximate Size:

FEMALE: head dark; thorax mostly yellow. The fourth segment of the abdomen entirely yellow, the others black, except for touches of whitish-yellow on the sides of the fifth segment and the posterior corners of the third. The tip of the abdomen usually brownish.

MALE: top of head covered with yellow pile. Thorax yellow. The first abdominal segment and the sides of the fifth and sixth, yellow.

FEMALE: length, 16 mm.; wing expanse, 36 mm.

MALE: " 13 " " " 33 "

B. Life-cycle:

The females of this species appear about a month later than the queens of their hosts, *B. affinis* and *B. terricola*—my earliest record is May 6. The males and young females are produced chiefly in August, but I also have a few records for July and September.

C. Hosts:

In the vicinity of Boston, the chief host of this *Psithyrus* is *B. affinis*, and the secondary host, *B. terricola*. Of 36 colonies of *B. affinis*, I found 11 to be parasitized, but of 14 colonies of *B. terricola*, only 2. However, in certain parts of North America where *B. affinis* is rare, and *Ps. ashtoni* and *B. terricola* are common, the latter, no doubt, serves as the chief host of this parasite.

D. Favorite Flowers:

I have seen the females of *Ps. ashtoni* on rhododendron, Pieris, and mountain laurel, and the males on buttonbush, sweet pepperbush, and boneset.

E. General Remarks:

It will be interesting to determine whether this *Psithyrus* breeds in the nests of species other than those belonging to the *Terrestris* group.

2. *Psithyrus fernaldae* Franklin (Fig. 18)

Synonym: *tricolor* Franklin

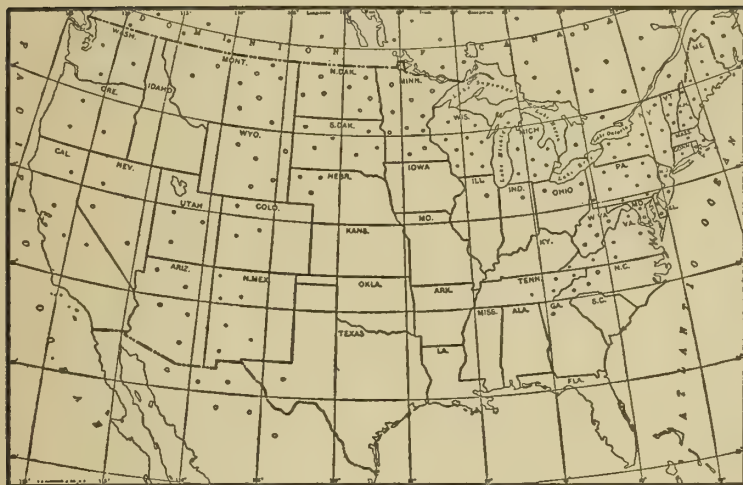


FIG. 18. Geographical distribution of *Psithyrus fernaldae*.

A. Coloration and Approximate Size:

FEMALE: thorax yellow, sometimes with a black interalar band. The fourth segment almost entirely covered with yellow pile. The rest of the abdomen black, except for touches of yellow on the sides of the first segment, and the apical border of the third. The tip of the abdomen with considerable brown pile.

MALE: top of head bearing yellow pile. Thorax like that of the female. The first and fourth abdominal segments entirely yellow; the second and third yellow and black in varying proportion. Segment five black, the rest of the abdomen brownish-yellow.

FEMALE; length, 14 mm.; wing expanse, 34 mm.

MALE; " 12 " " " 28 "

B. Life-cycle:

Although *Ps. fernaldae* is not rare in certain parts of New England (cf. *Bull. Mus. Comp. Zoöl.*, Vol. 67, p. 285), I have never taken a specimen in the vicinity of Boston.

C. Hosts:

The host of *Ps. fernaldae* is not known, but judging from the rather close study which Professor W. M. Wheeler has made of the bumblebee fauna near his summer home at Colebrook, Conn., it seems possible that this *Psithyrus* is parasitic on *B. perplexus*.

D. Favorite Flowers:

Since many of the *Psithyri* visit similar flowers, it is probable that *Ps. fernaldae* is no exception to this rule.

E. General Remarks:

In the females of this species, the abdomen is sharply pointed and curved forward below the venter.

3. *Psithyrus insularis* Smith (Fig. 19)

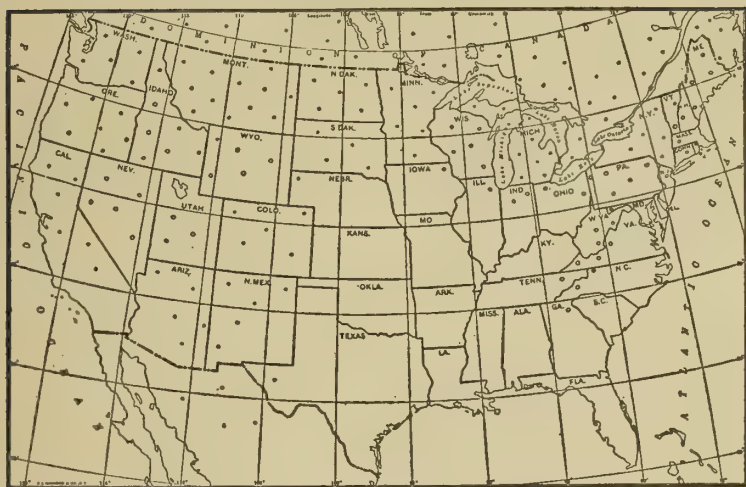


FIG. 19. Geographical distribution of *Psithyrus insularis*.

A. Coloration and Approximate Size:

FEMALE: face and head usually bearing considerable yellow pile. Thorax yellow, with a black interalar band. Abdomen black, with yellow pile on the sides of the third, fourth, and fifth segments.

MALE: head and thorax colored as in the female. Abdomen black, with yellow pile on the first three segments, and on the sides of the fourth and fifth.

FEMALE: length, 19 mm.; wing expanse, 38 mm.

MALE: " 13 " " " 33 "

B. Life-cycle:

This rare New England species apparently does not occur in the vicinity of Boston.

C. Hosts:

According to Sladen (1915), this *Psithyrus* breeds in the nests of *B. flavifrons*.

D. Favorite Flowers:

This *Psithyrus* belongs to the same group as *Ps. laboriosus*, and hence probably frequents similar flowers.

E. General Remarks:

Since *Ps. insularis* is found in parts of North America where *B. flavifrons* does not occur, it is evident that this *Psithyrus* has more than one host.

4. *Psithyrus laboriosus* Fabricius (Fig. 20)

(Including its variety *citrinus* Smith)

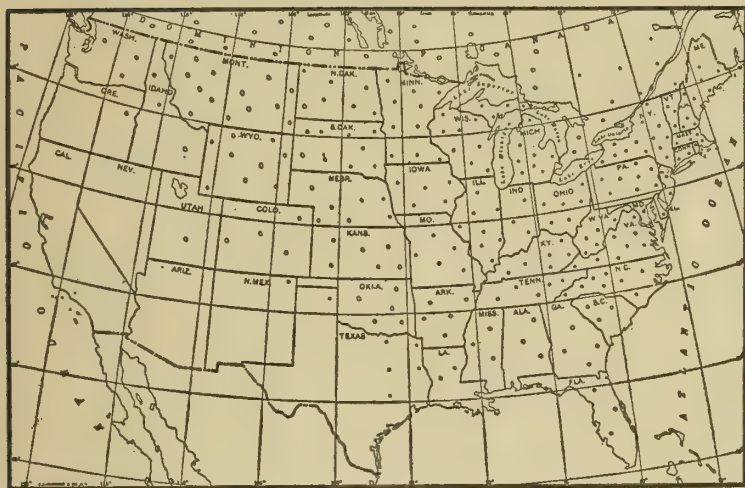


FIG. 20. Geographical distribution of *Psithyrus laboriosus*.

A. Coloration and Approximate Size:

FEMALE: top of head and thorax yellow. Abdomen entirely black, except that some specimens have touches of yellow on the sides of the third segment.

MALE: top of head with considerable yellow pile. Thorax and first two abdominal segments yellow; the remainder of the abdomen black. Not infrequently, however, specimens occur in which the yellow pile on the second segment is mixed with black, while in others a touch of yellow may be present on the third segment.

Variety *citrinus*:

FEMALE: like typical *laboriosus*, except that the third abdominal segment is entirely yellow.

MALE: third abdominal segment yellow, or with a slight admixture of black hairs; otherwise like the typical form.

FEMALE: length, 18 mm.; wing expanse, 38 mm.

MALE: " 13 " " " 33 "

B. Life-cycle:

Ps. laboriosus, including its variety *citrinus*, is by far the most common *Psithyrus* in the vicinity of Boston. My earliest record for this species is May 28. The males and young females are produced chiefly in August and September.

C. Hosts:

I have found this *Psithyrus* breeding in the nests of *B. vagans* and *B. impatiens*. Of the 49 nests of *B. impatiens* which I took, 7 were infested by the typical form of *Ps. laboriosus*, while 5 out of 15 nests of *B. vagans* were parasitized by its variety *citrinus*. It will be interesting to ascertain whether this specificity of hosts always holds true.

D. Favorite Flowers:

I have seen the females on rhododendron, high-bush blueberry, red clover, and purple vetch; the males on sumac, sweet pepperbush, boneset, and asters.

E. General Remarks:

The females of typical *Ps. laboriosus* are as a rule somewhat smaller than those of its variety *citrinus*.

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